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Biology of the Woodlark *Lullula arborea* (LINNAEUS, 1758) *(Aves)* in the Rzepin Forest (Western Poland)

[Pp. 61—160, pls XII—XXI and 41 text-figs]

Biologia skowronka borowego *Lullula arborea* (LINNAEUS 1758) *(Aves)* w lasach rzepińskich (Polska Zachodnia)

Биология лесного жаворонка *Lullula arborea* (LINNAEUS, 1758) *(Aves)* в Жепинских лесах (Западная Польша)

Abstract. In the Rzepin region the arrival of Woodlarks falls at the end of February and in the first half of March. They take possession chiefly of young pine plantations as their territories and the situation of their nests is to a great extent connected with the distance of the adjacent timber forest. They, as a rule, nest once a year, mostly in May and June. The nest is constructed by the female alone. It lays 2—6 (on the average 3·97) eggs. The average measurements of eggs are 20·63×15·77 mm. Fourteen-day egg incubation is performed by the female only. After the hatching of the young the egg-shells are eaten by the parents and so is the greater part of the faeces of the young. Nestlings are fed by both the male and female. They leave the nest between the 10th and 13th day of life; next they keep to small family flocks. The birds depart from the region at mid-October. Their main food constituent consists of insects (larvae and imagines), among them a large number of forest vermin; these are followed by spiders and seeds (chiefly those of pine and grasses). Losses of eggs and nestlings are remarkable. The mean number of fledglings leaving the nest is 1·85.

CONTENTS

I. INTRODUCTION

A great many authors wrote about the Woodlark, but I shall name only those who gave extensive and close studies to its biology, i.e., Koffán (1960) in Hungary, Krampitz (1952) in Germany, Koch (1936) in Holland, Labitte (1958) in France and Steinfatt (1939) in the U.S.S.R. The publication by Koffán (o. c.) is particularly worthy of mention. He devoted 18 years of his life to the study of Woodlarks, giving special attention to population problems. He was also the first to study in detail the structure of their nests and nest-holes in the ground. Krampitz (1952) laid stress on the ethology of the Woodlark from its arrival till the time when the young have left the nest.

No detailed papers on the biology of Woodlarks have hitherto been published in Poland, and the results obtained by the above-mentioned authors are not always compatible with each other. For this reason, at the suggestion of Prof. J. Sokołowski, I took up the study of the biology of Woodlarks and carried it out at Rzepin, near my habitation.

I wish to express my gratitude to Prof. J. Sokołowski for his interest in the progress of my study and valuable instructions. I am also indebted to Doc. Dr J. Pinowski for giving me the opportunity to get acquainted with the literature of this subject and advice. I also thank Mr. Mr. B. Aleksandrowicz, J. Bronowski, J. Czwojdrak, K. Danieluk, R. Domieradzki, W. Glinka, B. Jakuczun, S. Kaczor, K. Kanecki, F. Klimaszewski, W. Kostka, J. Mikajewski, W. Momot, Z. Osmólski, T. Pampuch, L. Pilc, L. Rachwał, A. Sachanbiński, A. Siciński, K. Sierakowski, C. Sierpiński, J. Sobieraj, M. Sójka, B. Więckowski, S. Wojciechowski and L. Ziółkowski for their enthusiastic assistance during my field studies.

II. METHOD

In the years 1962—1966 I examined more or less in detail 51 pairs of birds and 31 nests. Eleven nests were covered by continuous observation, lasting from dawn to dark. I watched them from a blind placed 1·0—2·0 m. from the

nest (Phot. 1). One nest (No. 15) was watched from a blind situated at the edge of a young stand 12 m. from the nest so as to check the method used. The construction of blinds was based on materials given by BUSSE (1960) and GRACZYK (personal communication). In the pre-nesting period the birds were watched 1. from among the tress surrounding the area occupied by them, 2. from blinds situated in different places in such areas, and 3. keeping quiet, from an unscreened stand at the edge of the area. This last manner appeared to be the best in the pre-nesting period. I used 10 × 50 and 16 × 50 fieldglasses for watching. In order to discover the site of a nest or to flush Woodlarks from their feeding grounds, I and my co-workers walked scattered, combing the area.

Watching was done for 35 daylong and 5 half-day periods (575 hours) at the time of incubation and for 80 daylong and 6 half-day periods (1240 hours) during the nestling stage, the total time of continuous watching being more than 1800 hours. This figure does not include a large number of days devoted to watching before and after the nesting season.

Eggs and nestlings were weighed using semi-analytical field scales to an accuracy of 20 mg. generally at the same time of day, namely, in the afternoon. The time was chosen so as to frighten the females least.

Food provided by the birds to their nestlings was determined by direct observations of feeding. The results obtained were next checked by the KLUIJVER (1933) method, i.e., by determining food components taken out of nestlings' gullets. At the same time, observations made from blinds rendered it possible to determine the size of rations given the young by their parents.

The quality and quantitative composition of material used for nests was examined after the young birds had left the nest, whereas measurements of nests and ground-holes were taken in the field at the time of particular stages of building.

III. HABITAT

The woods of the Rzepin region are fairly uniform and make up a complex of pine forests, which spread over an area of some dozens of square kilometres, including the forestries of Rzepin, Słubice, Radzików, and Polska Wola in the Słubice-on-Odra District, Zielona Góra Province. My investigation covered the forestries of Słubice, Radzików and Polska Wola and continuous watching was conducted in the forestries of Racławice and Zielona Góra, which belong to the Forest Administration District of Polska Wola. Owing to the poor differentiation of soils, the pine forests of these regions are very much alike in the nature of crops. Slightly moist soils prevail here, sands with a very small admixture of clay, on which even-aged one-species pine forests grow. There is only a small proportion of the oak in the undergrowth.

The intensification of wood exploitation after the war caused a remarkable

increase in the felling area, which brought about ecological changes favouring the nesting of larger numbers of Woodlarks.

Immediately after a forest has been cut down, trunks of trees as well as piles of logs, slivers, and branches are left scattered all over the area and the ground is littered with twigs broken off at the time of felling. Such areas do not yet form suitable breeding conditions for Woodlarks but, being inhabited by lots of insects and spiders, provide them with abundant food supplies. Later on, the preparation of soil and afforestation successively change the nature of environment, creating nesting conditions first for birds typical of steppes and areas covered with detritus (e.g., Skylark and Wheatear) and next for forest birds. The Woodlark, as a forest-steppe species, finds particularly favourable conditions here.

Table I

Phytosociological Record of a 3-year Pine Plantation with an Area of 100 Sq. M. (state at the end of March, before the commencement of vegetation)

Plant	No. of Tufts	Total Surface Area Overgrown, in sq. m.	Percentage Share in the Plant Cover of the Area
Carex ericetorum	55	4·540	64·1
Luzula campestris	80	1·412	19·9
Dactylis sp.	2	0·251	3·5
Calluna vulgaris	7	0·496	7·0
Festuca ovina	22	0·173	2·5
Deschampsia flexuosa	18	0·141	1·9
Juncus sp.	2	0·063	0·9
Hypericum perforatum	1	0·009	0·1
Weingaertneria canescens	1	0·005	0·1
Total	188	7·089	100·0%

Table II

Plant Species Serving as Shelter for Woodlarks' Nests

Plant Species Sheltering Nest	No. of Nests	Percentage of All Nests Examined
Deschampsia flexuosa	3	10·3
Calamagrostis epigeios	1	3·5
Festuca ovina	2	6·9
other *Gramineae*	10	34·5
(grasses altogether	16	55·2)
Carex ericetorum	9	31·1
Vaccinium myrtillus	2	6·9
Pinus silvestris	1	3·4
Carpinus betulus	1	3·4
Total	29	100·0%

The clearings are put to afforestation. In the first year the soil is prepared by paring the turf off by means of a plough in long parallel strips running right across the area, 1·20 m. apart. The pared-off pieces of turf cover the green strips of vegetation left between them. Thus the whole plant cover of the floor of the cut-down forest becomes destroyed. In the year of forestation no other plants grow in this area. Tufts of vegetation do not appear on the strips of pared-off turf till the next year, when *Luzula campestris*, *Carex ericetorum*, *Festuca ovina* and *F. rubra* are the first to spring up. In the second year after the planting of pines the vegetation consists of *Luzula campestris* (35%), *Carex ericetorum* (50%) and *Festuca* (15%). At the same time *Rumex acetosella* appears in the interspaces. *Deschampsia flexuosa*, *Juncus*, *Weingaertneria canescens*, *Calluna vulgaris*, *Hypericum perforatum*, etc. add to the composition of the plant cover in the next years. In some plantations *Chamaenerion*

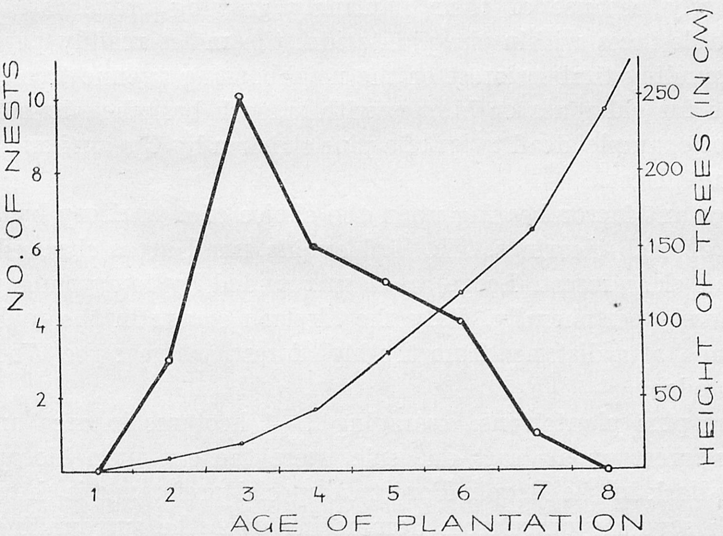


Fig. 1. Effect of the age of pine plantations on the distribution of Woodlarks' nests. The thick line represents the number of nests, the thin line the height of pines

angustifolium appears in masses in the third year. The share of *Carex ericetorum* increases to the extent that it forms strips, some dozen metres long, in both nooks of ploughed-out furrows. Table I shows the results of a phytosociological record of this environment. Last year's dry tufts of *Carex ericetorum* form almost only shelter for Woodlarks' nests in some plantations early in the spring. Table II shows the degree to which various plants partake in the screening of nests of the Woodlark.

In the next years the young pines grow bigger and bigger and Woodlarks nest only in gaps left between them and caused by, e.g., faulty planting, the action of harmful insects, etc. as well as near roads, paths and forest vistas.

In the end, however, the height of trees is such that they interfere with the orientation of birds so much that seven-year plantations are completely avoided by them. The Woodlark finds the optimum conditions in two-year pine plantations, i.e., in the third year after the felling of the old crop. In the next years the number of birds nesting in them decreases gradually (Fig. 1).

The Woodlark distinguishes itself from other species of the family by its habit of perching on tree-branches, serving it as observation posts, from which the male has an extensive view of the surroundings. For this reason the presence of such trees is one of the conditions of the choice of a nesting territory. Out of the trees growing in pine plantations, the small leafless ones with possibly horizontal thin twigs, suitable for the bird to take hold of with its toes, best fit the purpose. Such trees must overlook the surroundings, which condition is fulfilled, e.g., in the case of a young oak-tree, one metre and a half high, in a 3- or 4-year pine plantation. The Woodlark avoids young birches almost entirely because of their slantingly growing branches. Where there are no suitable trees within the plantation, the males readily perch on those of the surrounding timber forest or the neighbouring avenue trees. They show a preference for old pines or birches with smooth branches devoid of needles or leaves. For example, dead twigs of a pine stricken by *Cronartium asclepiadeum* are favourite places.

An important factor bearing upon the choice of a territory by a Woodlark is the area of such clearings. The bird avoids small areas situated amidst an old high and close forest. Large areas surrounded by low young growths are occupied merely peripherally. Only the Skylark occurs in the middle of such large clearings, at a distance from the high forest, whereas the Woodlark nests close to its edge.

Two-year pine plantations, averaging 2—4 hectares in area and adjacent to an older forest on at least one side, were the optimum biotope occupied by the Woodlark in the Rzepin Forest. A special preference is shown for plantations with several young trees dominating over the surroundings.

The foregoing environments inhabited by the Woodlark in the Rzepin Forest do not as a rule differ in character from those described by other authors, e.g., Koffán (1960) and Sokołowski (1958). The pine plantations under description constitute a similar type of biotope for several consecutive years in spite of changes brought about by succession in the composition of their herb layer at the same time. This lasting nature of the biotope is emphasized by Bruns (1956), Koffán (1960), and Witherby et al. (1948) as one of the conditions for occupation of nesting territories. Bruns (o. c.) reports the nesting of Woodlarks in vineyards and orchards, which environments of the cultivated landscape fulfil the condition of stability of the biotope and at the same time provide many convenient observation posts. The importance of these details for the occurrence of the Woodlark is also stressed by Krampitz (1952) and Leutzinger (1955).

IV. SPRING ARRIVALS

The Lark is the earliest of the Polish breeding birds returning from their winter-quarters. According to Taczanowski (1882) and Sokołowski (1936), the Woodlark returns somewhat later than the Skylark. In the Rzepin region the appearance of Woodlarks falls for the most part in mid-March. The date of arrival depends on weather conditions, especially on the subsistence of snow cover (Table III).

Table III

Dates of Arrival of Woodlarks and Skylarks in the Rzepin Region against the Background of Weather Conditions

Dates of Arrival of the First		Difference in Days	Weather Conditions Preceding the Arrival of Birds
Woodlarks	Skylarks		
17. 3. 1962	4. 3. 1962	13	
13. 3. 1963	7. 3. 1963	6	6—8·3. snow cover, lying for 73 days, is thawing
14. 3. 1964	25. 2. 1964	18	frost up to 12.3.
14. 3. 1965	—	—	
21. 2. 1966	20. 2. 1966	1	20.2. thaw
26. 2. 1967	18. 2. 1967	8	11.2. thaw

The arrival of Woodlarks is hard to notice. They return in flocks, keeping silent. When disturbed, they deliver a trill, completely unlike the alarm call of these birds after they have been paired. Only a thorough inspection of the area makes it possible for the observer to determine the time of their arrival. It is not before the sun warms up the air that the males begin to sing short phrases, become offensive to each other, and visit the breeding area. Each year I observed flocks of Woodlarks in feeding grounds first, and next single males in breeding areas. Feeding in flocks was observed in the same places as in the autumn only that the birds showed a slight preference for pastures, meadows and winter-corn fields and avoided fallows, stubbles, and slopes of railway embankments. In the first week following the arrival of flocks, males may be seen regularly while flying over the last year's breeding areas. In one of the plantations I observed 2 Woodlarks standing side by side as early as February 26 in the year 1966. Unfortunately I was unable to judge from their behaviour whether they were a mated couple or two males. In the second week after arrival the first males usually occupy their territories. In the third week half the males have already female mates.

A sudden deterioration of weather conditions, e.g., a fall of snow that occurred on March 12 and 13, 1966 made the Woodlarks move to the suburban areas. On March 15—16 the persisting unfavourable conditions (5-centimetre

snow layer and cold wind) caused the formation of parties of 10—12 specimens each, though the birds had already associated in pairs before. These parties left the breeding haunts and approached the farm buildings, but they were never seen in the farmyards. When the weather became warmer again, the parties broke up and the birds returned to the territories occupied previously. NAUMANN (1900) published analogous observations made in this very region (Rzepin) on March 18—25, 1887.

V. CHOICE OF TERRITORY AND PAIR FORMATION

The nature of habitats chosen by Woodlarks in the Rzepin Forest has already been discussed in Section III. I observed the order of precedence in which the males took possession of particular areas. First they occupied old breeding territories or younger plantations adjacent to them. These were therefore 2- and 3-year-old pine plantations in the neighbourhood of felling sites, e.g., those under power lines. In such places singing males could generally be seen as early as 10 days after their arrival. Somewhat later they occupied areas uninhabited by Woodlarks in the previous year, as then these areas had not fulfilled the necessary conditions yet. They were new 2-year plantations. Next, usually in April, when the best terrains had already been occupied, the remaining males settled down in places which hardly met their requirements: old brushy felling sites, often very small in area, or older and so higher plantations. In the last case the plantations served as feeding grounds and the nest itself was sited out of them. These territories may be exemplified as follows: a 16-are area left after the liquidation of a tree-nursery bordering on a 6-year pine plantation, an old pine forest in the neighbourhood of 9- and 1-year plantations, a discontinuous timber-forest and, in the end, a 30-are 4-year plantation situated among young pine stands, more advanced in age. In these areas males appear and find their mates latest. In two extreme cases males were mateless up to the end of May.

After arrival the males keep silent and the commencement of singing is controlled by weather, especially by day temperatures. At first they sing slightly, utter short phrases, and fly over the territory from one side to the other. Lastly, on sunny days they proclaim the occupation of the territory with continuous singing and flying large circles round it.

The size of Woodlarks' territories ranges from 20,000 to 30,000 sq. m. and thus it is 3 times as large as that of Skylarks (7,000—11,000 sq, m.) in the same region. A medium-sized plantation, up to 3 hectares in area, was usually occupied by one male, whereas larger plantations, 3—5 hectares, were shared between two males. In the Rzepin Forest such plantations have generally the shape of elongated rectangles. If they are occupied by two males, the boundary between their territories runs along a diagonal. The neighbouring males sing without regard to each other and rarely drive each other off on the border, but the appearance of strangers in their territories usually stops

them from singing and they drive the strangers away. The notes uttered by the birds when they chase each other are more grating and coarse and accompanied by the clacking of bills.

Towards the end of March females appear in the territories. At first the male responds to the appearance of a female by stopping its song, it dives towards the female and drives it away. In the end, however, it allows the female to stay in its territory. From that moment the male takes to the air rapidly and after singing always alights by the side of the female. The united pairs do not part for a while. The intensity and continuity of singing, as well as the height which the birds reach, when they are on the wing, are smaller than before. The main activity in the daytime, apart from the male's singing, is the exploration of the territory occupied. The larks look under almost each tuft, feed and peck about it. The female evidently plays a leading part and is followed by the male, which stops at higher spots, on a tree-stub, clod or stone, to examine the area. They, besides, behave so quietly that it is hard to notice them. It is only when the male sees danger, e.g., a man at a distance of 20—30 m., that it utters alarm calls, to which the female replies.

The behaviour of males in connection with their occupation of territories described by KRAMPITZ (1952) is analogous with that presented above. In his description of pair formation this author directs attention to the fact that the female, when driven off at the first meeting, retreats to a neutral area for a short time.

The pairing of Skylarks *Alauda arvensis* proceeds in a similar manner (DELIUS, 1963; PÄTZOLD, 1963).

VI. NOTES AND SONGS

1. Notes

A. Call note. This is the best-known note, by which the Woodlark can be recognized at any season of the year (SOKOŁOWSKI, 1925). The bird utters these notes in its own territory and in visited places, on the wing and at its observation post, when foraging, resting, incubating eggs, feeding and leading nestlings, and after the breeding season. The call consists of two, exceptionally, three syllables, but its monosyllabic variant can also be heard. It is difficult to transcribe these notes, as they vary even in the same bird and sound once *d'dlui*, *t'tluiii* and *d_{it}-tlui*,, another time tew leet or only fragmentary *dli*, *tli*, and *lui*. The intensity of the call notes varies with the distance between the two birds; in the vicinity of the nest the call is inaudible at a distance exceeding 5 m. The variants *dli*, *tli*, and *lui* prevail in these calls, uttered in a very low voice. The male calls lowest, when it perches in the watch-tree in the close neighbourhood of the nest; the female delivers the lowest notes, when it is having a day nap in the nest.

B. The alarm call resembles the call notes, from which it is distinguished by accent. The bird stresses the last syllable and does it the more strongly, the more excited it is. In such cases the alarm call often consists of 3 syllables, of which the two final ones bear the accent. It sounds like *didluiit, tch'tui,* or *t'tluiluit,* the form *tch'tui* being the commonest. The first part does not resound for a long distance, but the ending *uii* is very sonorous. The birds usually utter these notes from the ground, less frequently on the wing, mainly in their territories and particularly often in the period of fights of males for territories. In the transcription presented by German authors (NAUMANN, 1900; NIETHAMMER, 1937, and others) the call didloid is often repeated. This record does not render the actual sound. WITHERBY et al. (1948) interpret it better as *tituit* and VOIGT (1940) as *di*$_{ae}$*liht.*

C. Call of anxiety. At a distance from the nest and after the breeding season this note is heard only sporadically. Along with the call note, this is the commonest call given by birds, when they approach the nest with food. It is particularly often uttered by the male coming to the incubating female. Both birds answer each other using these notes and then pass to the call notes, as they get reassured. The call of anxiety is dissyllabic, has a falsetto sound, and undergoes no individual variation. It is not sonorous. Its first part is lower than the second, and it may be most accurately recorded as *pri*^{heet}.

No special notes are produced by Woodlarks when they are in the state of evident fear, which they express by an alarm call or that of anxiety, or most frequently by both these notes delivered alternately.

D. Call of anger. The Woodlark manifests anger relatively rarely. The call of anger can oftenest be heard when males chase each other from their territories in the presence of the female and when they fight against the birds of other species (Starling, Yellow-hammer). It resembles the hiss of young Starlings, is harsh and occasionally ends in a clack of the bill.

E. Flock call. In the period when Woodlarks gather in flocks, they express their fear by a trill which may be derived from the first part of the call of anxiety presented above and may be described as a *peerrr.* After a call of one of the birds the rest usually join in and take wing. This is thus an alarm call and at the same time a signal for departure.

2. Songs

A. Analysis of song — its components. On the basis of the motives used in the song of the Woodlark I have distinguished 5 phrases in it. They differ not only in sound but also in rhythm:

1. Slow low dissyllabic motives *di lee, de lee, de lee, d'lee d'lee...*

2. Somewhat faster high dissyllabic motives *dee yah, dee yah, diyah, diyah, dyah...*

3. Low monosyllabic *loo loo loo loo loo...*
4. Higher monosyllabic *dli dli dli dli dli...*
5. Fast trill *lilililililili...*

Figure 2 shows the percentage share of the particular phrases in the song. As will be seen from it, the monosyllabic phrases form 50—81 % of the song and the dissyllabic ones 19—41 %. The share of the trill is the smallest (0—9 %). The high monosyllabic phrases dli dli dli are the commonest (40—45 %) and followed by the low monosyllabic phrases loo loo loo in respect of frequency.

The number of motives in a phrase fluctuates, which may be exemplified by the results obtained for 40 phrases of tree songs of one and the same male (Table IV). It appears that the mean numbers of dissyllabic motives in the phrases are the lowest (6·9), the high monosyllabic motives dli dli dli having the highest mean value (11·2).

The time taken by the same male to sing each of the 32 phrases measured is given in Table V. The differences in time are remarkable and reach 19 seconds. The arithmetic mean calculated from the differences is 9·7 seconds and the commonest duration of a phrase (modal mean) is 8 seconds.

Table VI illustrates the succession of phrases in a few different songs of the Woodlark. It suggests that there are no distinct rules governing the sequence of phrases.

Listening intently to a song of the Woodlark one can find its resemblance to some phrases of the songs of the Tree Pipit and Iterine Warbler. However,

Table IV

Number of Motives in Particular Phrases of the Same Male Singing in a Tree

Kind of Phrase	No. of Motives in Phrase								No. of Measurements (N)	Arithmetic Mean (M)
	5	6	7	8	9	10	11	12		
dissyllabic	4	1	4	1	2	1	—	—	13	6·9
looloolooloo	3	—	4	7	1	1	1	—	17	7·6
dlidlidlidli	—	—	—	—	—	2	—	2	4	11·0
trill	—	—	—	1	1	1	2	1	6	10·2

Table V

Duration of Phrases in the Woodlark's Song

Duration of One Phrase (in sec.)	4	5	6	1	8	9	10	11	12	13	14	15	16	17	18	19	Total
No. of Phrases	1	5	2	2	6	1	3	3	2	1	1	1	1	2	—	1	32

Mean duration M = 9·7 sec.
Commonest (modal) duration M_0 = 8 sec.

Table VI

Order of Precedence of Phrases in the Song of the Male Woodlark

Phrases: 1 — *di lee, de lee, de lee, d'lee, d'lee...*
2 — *dee yah, dee yah, diyah, diyah, dyah...*
3 — *loo, loo, loo, loo, loo, loo, loo...*
4 — *dli, dli, dli, dli, dli, dli, dli...*
5 — trill: *lilililililili...*

Different songs
1 . 5 . 1 . 4 . 3 . 3 . 1 . 3 . 5,
4 . 3 . 2 . 2 . 3 . 4 . 1 . 4 . 3 . 1,
1 . 4 . 4 . 4 . 4 . 4 . 3 . 2 . 3 . 4 . 4 . 5 . 5 . 5 . 1 . 4,
4 . 4 . 4 . 2 . 5 . 1 . 1 . 1 . 5 . 2 . 2 . 3 . 5,
4 . 1 . 4 2 . 3 . 4 . 1 . 3 . 5 . 4 . 2 . 2,
1 . 4 . 3 . 3 . 4 . 1 . 2 . 4 . 4 —, 1 . 3,

the influence of the Woodlark's song on the songs of other birds from the same environment observed in this region is remarkably greater.

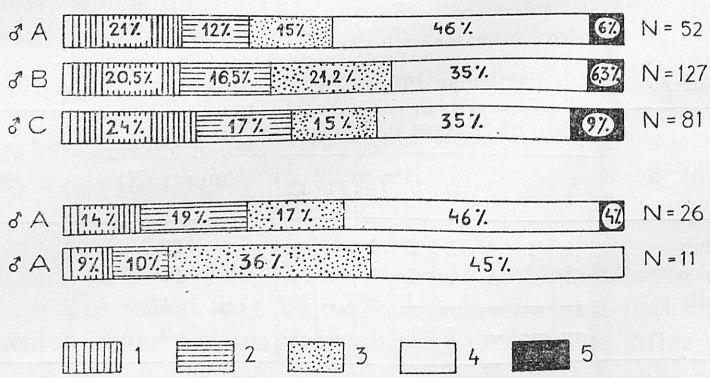


Fig. 2. The share of particular phrases in the Woodlark's song. The upper graphs refer to songs in flight, the lower ones to tree songs. N — number of phrases in the whole song analysed, 1 — slow low dissyllabic motives, 2 — somewhat faster high dissyllabic motives, 3 — low monosyllabic, 4 — higher monosyllabic, 5 — fast trill (see page 70—71)

The division of the Woodlark's song into phrases and motives presented above agrees with the results obtained by Voigt (1940). The existence of 5 motives and practically endless possibilities of combinations of various phrases (cf. Table VI) contradict the opinion put forward by Heinroth (1926) that the song of this bird is poorly diversified.

Considering the similarity of the Woodlark's song to those of other birds, KRAMPITZ (1952) writes about its imitation of notes of the Swallow, Great Tit, Skylark, Chiffchaff, and even of a whole song of the Tree Pipit. In the Rzepin Forest all the male Woodlarks repeat a phrase similar to one of the phrases of the Tree Pipit. It constitutes 10—19% of the song (Fig. 2). In the spring this phrase can, in addition, be heard in the forest a few weeks earlier than the song of the Tree Pipit, which seems to indicate the inherited ability of the Woodlark to reproduce this phrase. The resemblance of a fragment of the song of anxiety (see Point F of the present subsection) to some fragments of the Icterine Warbler may be explained in the same way.

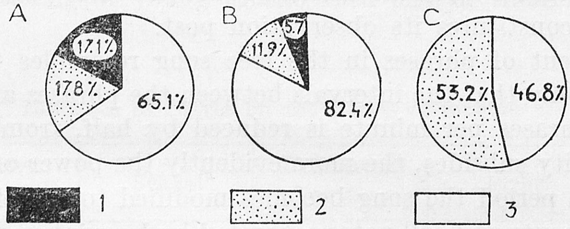


Fig. 3. The effect of the stages of breeding on the share of particular forms of singing: A — unmated males, B — after mating but before nest building, C — during incubation. 1 — song from ground, 2 — tree song, 3 — song in flight

B. Song in flight. This is an essential form in which the bird proclaims its presence in the period preceding pairing. This kind of singing is the commonest in and typical of all larks. It prevails both in single males looking for females and in the first period after pairing, giving way to the tree song (song uttered from a tree) as late as the incubation period (Fig. 3). When rising, the male does not start singing until it has transcended the height of the neighbouring trees. This behaviour would indicate that the bird does not feel safe low above the ground and, being originally a steppe species, recaptures the feeling of security when it has ascended above the surroundings. The singing male rises higher and higher and describes circles, 30—80 m. in diameter, in which it differs from the Skylark.

The height of flight varies largely during a song. The upper flight limit is 100 m. for single males and does not exceed 50 m. in the case of paired males. The downward flight is not commonly as vehement as that of the Skylark. The Woodlark usually begins to drop faster at the height of the tops of neighbouring trees. The song in flight is often combined with the preceding or the following song uttered from a tree or from the ground. The song in flight usually lasts 2 minutes, which is true of both paired and single males. These last can prolong their songs up to 70 or even 94 (!) minutes in the full singing period. In several cases I heard songs lasting longer than 1 hour. There is no other European bird that might boast of such a long and almost uninterrupted song and, what is more, performed on the wing. According to KRAMPITZ (1952),

the differences in height of flight and length of song between a single male and a paired one, being constant, permit the investigator to distinguish them one from another.

The foregoing observations, concerning the rise in the song-flight, the commencement of singing and the speed of dropping, thoroughly confirm the data presented earlier by VOIGT (1940), but the length of song now recorded considerably exceeds all the records in literature (HEINROTH, 1926; KRAMPITZ, 1952).

C. Tree song. This form of singing distinguishes the Woodlark from the Skylark. However, it does not become predominant until the female's incubating the eggs (Fig. 3). Then the male sings for the most part sitting on a twig of the tree that constitutes its observation post.

The arrangement of phrases in the tree song resembles that in the song in flight (Fig. 2) only that the intervals between the phrases are longer. Hence, the number of phrases per minute is reduced by half, from 8·7 to 4·4. The more sexual activity subsides, the more evidently the power of voice decreases. In the incubation period the song becomes modified to the effect that it consists of song fragments and call notes separated by long intervals. These phrases are uttered in such a low voice that they are inaudible at a distance of more than a few metres.

D. Song from ground. This song is performed by both single and paired males. It is connected with their marking out territories and that is why it vanishes when the female has incubated for several days (Fig. 3c). This song is usually the first to ring, when the male awakes in the morning, and it is also its last song before the day ends. When the weather is unfavourable it replaces the song in flight. The song from the ground is generally short, it lasts from several seconds to 14 minutes, most commonly 1—2 minutes. The intervals between particular phrases are longer, up to 1 minute.

E. Song during chase. This is a variant of the song in flight, uttered more vehemently and alternated with calls of anger. It is stimulated by the appearance of anether male in the occupied territory at moments of intense sexual excitement.

F. Song of anxiety. This is a variant of the previous song and is always associated with danger threatenig from somewhere on the ground in the vicinity of the bird's residence. The bird utters this song, when it gets frightened by a man approaching to a distance exciting its desire of escape. During the song the female gives up its activity and remains dead still. In a while both the birds fly away. I have not heard this song outside the territory occupied by the Woodlarks or before and after the breeding season. Neither was it released by the sight of rivals or any other birds. In several cases, however, the male started this song at the sight of the female leaving the nest.

G. Song of females. It is sung by females which, when warming the nestlings, are forced to get off the nest because of the approach of the male. The female sings at a distance of 0·5—1·5 m. from the nest and interrupts singing to peck excitedly at the ground or to trim its feathers energetically till the male has left the nestlings. Trill phrases prevail in such a song and its measure is accelerated. Each phrase begins with a call note followed by a trill. From the ethological viewpoint the song of females may be regarded as equivalent to males' song of anxiety. Only once I observed a male singing in a similar manner near the nest, when the female reached the nest ahead of it to feed the young. Females sing fragments of this song as early as the autumn, after the first moult (Heinroth, 1926). My observations show that this song was sung from the hatching of young to the 10th day of their life.

Table VII

Influence of Drives on the Forms of Singing

Song \ Drive	Sexual	Defence of Territory	Fight	Escape
in flight	strong	moderate	moderate	no
tree song	moderate	strong	moderate	weak
from ground	no	moderate	moderate	moderate
during chase	strong	strong	strong	no
song of anxiety	no	moderate	no	strong
song of female	no	no	weak	strong

The first five types of songs are delivered by males only. They are heard in the mating season and manifest the sexual drive of the singer, its desire to fight or to run away. Males also use a song to proclaim the occupation of a territory. Table VII shows correlations between the Woodlark's drives and the types of its songs.

3. 24-hour Rhythm of Singing

The twenty-four-hour pattern of singing is governed by the bird's diurnal activity. The numbers of songs performed in particular hours of the day are different, as will be seen from Fig. 4. It shows that the Woodlark sings most frequently in the morning hours, the maximum of singing occurring, earlier in single males than in the paired ones. The singing intensity curve, or the length of singing in minutes per hour (Fig. 5), has a morning maximum at 7 o'clock in April and at 4 o'clock in June for single males (Fig. 6) and one hour later in the case of males that have a mate. At the time of the morning maximum the song lasts longest, it becomes shorter later into the day, often taking less than a minute. Paired males stop singing almost entirely at 10 a.m., whereas the single males show a slight increase in the intensity of singing just

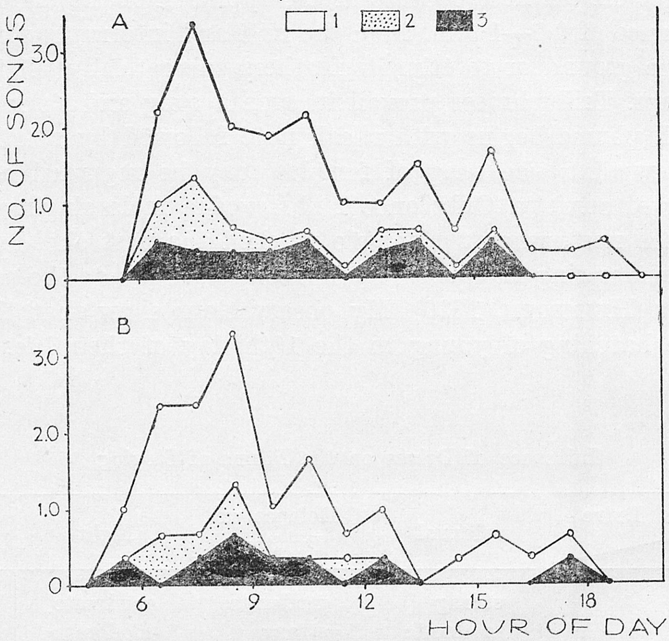


Fig. 4. Numbers of songs in particular hours of day in the case of unmated (A) and mated (B) males. 1 — song in flight, 2 — tree song, 3 — song on ground

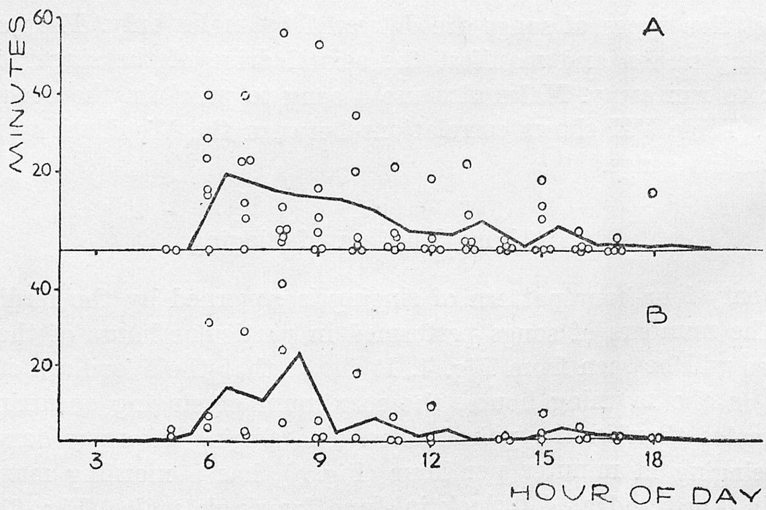


Fig. 5. Twenty-four hour pattern of intensity of singing in the case of unmated (A) and mated (B) males in March. The total lengths of singing of particular males in given hours of day are given on the ordinates. The solid line represents the mean for the given group

before sunset, especially in May and June (cf. Fig. 6). Thus, the rhythm of singing of the Woodlark differs from that of the Skylark, in which Delius (1963) observed the maintenance of the same level in the daytime, or even a certain increase in intensity up to 3 p.m.

Singing at night is another problem. At 10 p.m. on April 22, 1964 I happened to hear a short song of a male and again just after midnight on June 6,

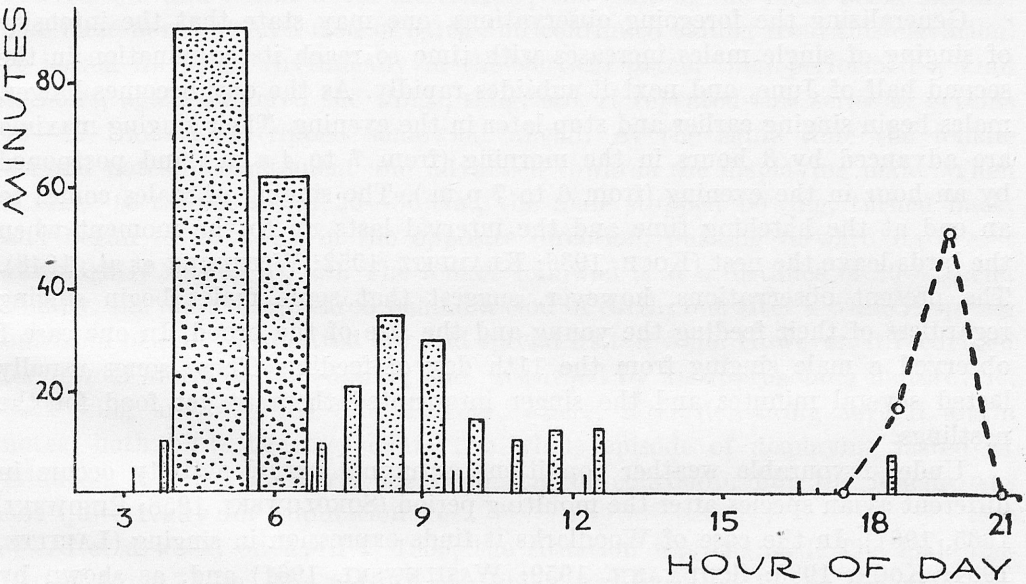


Fig. 6. Twenty-four hour pattern of singing of unmated male in June (one-day observations). The blocks illustrate the length of particular songs. The broken line shows the intensity of singing of the same male on the previous day (from 5 to 9 p.m.)

1966, but this time a long one. In both cases the night was dark and moonless. Labitte (1934) listened to night songs on June 17 and 20, when the first clutch of the bird had been destroyed. Sokołowski (1952) heard a Woodlark's song at midnight in calm warm nights in the Świętokrzyskie Mts. In view of the casual nature of this song the problem of its dependence on other phenomena is still open.

4. Seasonal Variation of Singing

The zeal for singing increases in the case of single males from March to June and thus as the temperature rises. The mating of birds brings about a steady drop in the intensity of singing. Although the number of songs undergoes no reduction in the incubation period, the duration of songs is shortened, those lasting 1—2 minutes being prevalent. The change in the type of singing is characteristic: the tree song constitutes from one-third to two-thirds of all the songs, whereas the song given from the ground is completely wanting

(cf. Fig. 3). Should the female perish unexpectedly, this process may be reversed One of the males, for instance, sang less and less, as the hatching time approached, but after its mate disappeared under unknown circumstances about 3 days before hatching, it began to sing more frequently without leaving the territory. When no other female had joined it in a fortnight, it sang as eagerly as all single males and even attained a record length of singing, equal to 94 minutes (Fig. 6).

Generalizing the foregoing observations, one may state that the intensity of singing of single males increases with time to reach its culmination in the second half of June, and next it subsides rapidly. As the day becomes longer, males begin singing earlier and stop later in the evening. Their singing maxima are advanced by 3 hours in the morning (from 7 to 4 a.m.) and postponed by an hour in the evening (from 6 to 7 p.m.). The singing of males comes to an end at the hatching time and the interval lasts up to the moment when the birds leave the nest (Koch, 1936; Krampitz, 1952; Witherby et al., 1948). The present observations, however, suggest that some males begin singing regardless of their feeding the young and the size of the brood. In one case I observed a male singing from the 11th day of feeding. These songs usually lasted several minutes and the singer interrupted them to get food for the nestlings.

Under favourable weather conditions autumnal sexual activity occurs in different avian species after the moulting period (Sokołowski, 1958; Pinowski, 1965, 1967). In the case of Woodlarks it finds expression in singing (Labitte, 1934; Koch, 1936; Schumann, 1959; Wasilewski, 1961) and, as shown by the present observations, in chasing each other. The autumnal song is usually short and can be heard on warm sunny days only. However, on slightly hazy but sunny days this song hardly yields in anything to the spring song. For example, on September 24, 1963 I heard 25-minute songs, and one lasted even as long as 34 minutes. These songs were given more frequently from trees than in flight or from the ground. According to Kumerloeve (1966), in Turkey, where the Woodlark is a roaming bird, the song of males is commonly heard as late as October. Taczanowski (1882) writes about a song of a male wintering in Poland, which he heard in January. Schumann (1959) states that in the autumn males generally sing in the morning, the afternoon phrases being short and abrupt.

VII. DISPLAY AND BEHAVIOUR TOWARDS RIVALS

For a long time the copulation of the Skylark, Crested Lark and Woodlark was known only from observations of laboratory birds (Howard, 1929; Stresemann, 1956, 1957; Abs, 1963). Delius (1963) studied the copulation of Skylarks under field conditions and Hoffman (1951) that of Woodlarks. The description given by Hoffman (o. c.) is, however, rather vague and combines copulation with the digging of a hole in the ground.

In spite of intense efforts I did not manage to witness the act of copulation and my observations cover only the display and other manifestations of sexual behaviour. In view of the lack of detailed descriptions in literature I shall quote some observations made by one of my collaborators, Mr. K. SIERAKOWSKI: On March 21, 1965, watching a pair of Woodlarks from the morning, he observed the display as late as 4·04 p.m. At first both the male and female uttered call and alarm notes alternately, the calls of the male being shriller. The male next got on a clod of earth and continued calling from this elevation. It jerked its wings rhytmically in the vertical plane, then performed a kind of bows, again quivered the wings, sang, etc. It repeated this series of actions 10—12 times and tripped somewhat ahead. At the same time the female uttered notes of excitement and advanced towards the displaying male. When it came to a distance of 20—30 cm., the male stopped bowing, turned back, and began to go away in the opposite direction, pushing forward its breast and slightly raising its tail. The female followed it at a distance of 20—30 cm. Finally, the male disappeared behind a clod of earth, but after a while it sprang out from behind it, squatted low and spread its tail wide. However, it recovered its normal attitude immediately and, disturbed by an approaching motorcycle, took wing and alighted 3 m. further, where, after delivering several alarm notes, both birds became silent. The whole episode of displaying lasted 11 minutes. It was, therefore, the beginning of courtship, but the female was not quite ready for copulation yet.

After a week, on April 6, 1965, the situation was changed. The male displayed from 7 a.m. The pattern of display was like that in the previous case only that the female, approaching the displaying male, assumed a posture provoking to copulation. It crouched and fluttered its wings. At that moment another male appeared and there developed a fight, which lasted, with intervals, from 8 a.m. till 1 p.m., and had an exceptionally fierce course, whereas the female stood aside.

In general, the forms of sexual behaviour of the Woodlark may be divided into the attitude of the male towards the female, the attitude of the female towards the male, and that of the male towards its rivals.

1. Attitude of the Male towards the Female

A. Qick rhythmical wing movements, performed with only the tips of the primaries in the vertical plane. They express an extreme excitement of males not only in the presence of females but also roused by the nearness of their rivals and other birds (Starling, Yellowhammer). The quivering of wings usually occurs as a preliminary form of display and it next accompanies the display proper. DELIUS (1963) describes it in the Skylark, observed under the same circumstances and during copulation.

B. Bows, made by the bird rather vehemently. In some respects they resemble the behaviour of pigeons. This kind of behaviour, too, is an expression

of excitement during fights as well as of anxiety roused by changes in the surroundings of the nest in the period of feeding the young. But then the bows are never so low and ritualized as at the time of display.

C. Turning away from the female is an obvious element of display. The male has its tail slightly erected, its plumage is puffed out and the head drawn back so that the bird looks dumpy in the figure. It also thrusts out the posterior part of its body. The female responds to this attitude of the male either by following it or by manifesting the readiness to copulate. A similar behaviour has also been found in the Skylark (Delius, 1963; Stresemann, 1956) and Crested Lark (Abs, 1963; Stresemann, 1957).

D. Turns. These accompany the preceding posture and seem to combine the male's expectation of the female's approach and its further turning away from the female. These movements have also been mentioned by Niethammer (1937).

E. Display "proper". It is induced by the highest sexual excitement of the male. It then crouches on the ground, with its plumage puffed out and the tail widespread, drops its wings and turns the head towards the female. The Skylark behaves in a similar manner (Delius, 1963; Stresemann, 1956), whereas the Crested Lark has a more upright position (Abs, 1963; Stresemann, 1957).

2. Attitude of the Female towards the Male

In addition to pursuing after the male, answering its calls, and going together round the territory, the female manifests its sexual excitement only by readiness for copulation. Then it crouches quivering its wings and approaches the male. The sight of the female in this posture releases a desire for copulation in the male.

3. Attitude of the Male towards Its Rivals

A. After pairing the male's agonistic behaviour in relation to its rivals manifests itself in the mildest form by its standing on an elevation of the ground with the plumage puffed out and by its trimming feathers in a nervous ritualized manner. In this way it announces to other males in the neighbourhood throughout the breeding season that the place is occupied.

B. If, however, in spite of that a strange male has appeared in its territory, the rightful occupant chases it away as far as the boundary of the territory. But in the case when the rival male will not leave the territory, the chase becomes more and more bitter. A peak of chasing falls in the period of copulation, after which the male becomes gradually more indifferent to the

presence of other males except for the beginning of the incubation period when it still chases them away. Immediately after the hatching of the young the males completely give up fighting. They often sing over another male feeding the nestlings without any evident response on its part, which indicates the complete expiration of territorialism of the male.

C. An extreme form of chasing is the threatening flight. In this flight the males keep a shorter distance between each other, fly exceptionally low above the ground, and express their excitement uttering the "song of anger". Two features make this flight different from normal: the hanging down legs of the male which defends its territory and the utterance of calls of anger at the moments of alert.

D. Fighting is the last argument used against a rival encroaching upon the territory. Although males reveal readiness for fighting during the whole breeding seasons and even when they are in autumnal flocks, they fight most bitterly in the period directly preceding their nesting. The intensity of fights is proportional to the frequency of the remaining forms of sexual activity and therefore they are an extreme expression of these forms. The birds fight on the ground or in spiral ascending flights to a height of several metres from the ground and they chase each other alternately. The fiercest attacks are delivered just above the ground. The birds try to assault each other usine claws or to grip with the bills. However, I have never observed any damags caused by them. It is worth while to quote a description of one of the fightg observed by Mr. K. Sierakowski, whom I have already mentioned above. Moreover, it is the same fight that he touched on in the above-presented description of display on April 4, 1965. The males approached each other, extended their tails and thrust forward the heads, shaking their wings energetically. Having come to a distance of 20—30 cm., they rose and in the air tried to push each other back, pressing breast against breast, or to grip each other with their bills. They took to the air to only a slight height from the ground. Such attacks were repeated four times, after which the birds flew away in different directions. After the battle the female followed its mate. Sixteen minutes later the birds attacked each other again and in the intervals between the battles they chased each other, making large circles 10 metres above the plantation. In the flight, different from that in which males are driven away from a neighbouring territory, they chased each other at a very short distance, singing continuously. Their voices were, however, more violent (song of anger) and the attacking male uttered notes resembling the hissing of young Starlings. Only once, for a fraction of a second, it touched the back of its adversary in the flight. The flights, however, did not appease their desire for fight and, having touched down on the ground, they resumed their attacks, flying up to each other. When one of the fighting males managed to reach

its adversary with the bill, this last bird squeaked but, though both of them flew in opposite directions, they soon started their fight again.

During these struggles they paid little attention to the presence of the observer, whom they let approach to a very short distance.

VIII. NESTS

1. Choice of Nesting Site

The habit of mated pairs to make common rounds of the territory occupied by them is connected with their marking-out of this territory, acquisition of food and selection of the site of the future nest. These activities take them the greater part of the day throughout the period from their joining in pairs till the incubation of eggs by the female. In the population studied by me this period lasts from the end of March to the beginning of the third decade of April, and so for 3—4 weeks. However, as early as the beginning of the second half of this period the birds keep constantly to one part of the territory, in which they spend the nights and start to scrape out holes for the nest. Their roost can easily be recognized by a large amount of faeces accumulated in one place, light in colour against the dark humus substratum (Phot. 2).

The choice of site is not incidental, though it depends on topographical details that are hard to distinguish. The place in which the Woodlark builds its nest is for the most part situated in a peripheral part of the territory. This situation of the nest results from the biotopic requirements of the birds. The Woodlark, being associated with parkland-type environments or with a forest margin, does not place its nest in an open area as the Skylark does. The nearness of trees, mentioned above in the description of the biotope, is an indispensable condition for the choice of a site, although old timber forests are avoided. The height of the nearby growth is the most decisive factor as regards the distance of the nest from the edge of the territory, namely, the higher the trees, the farther from them the nest is situated. This correlation is illustrated in Figs. 7 and 8. The graph in Fig. 7 shows it in the aspect of the angle formed by the horizontal line and the line connecting the eye of the female sitting on the nest with the tops of the nearest trees, which angle in most cases ranges between 15 and 45°. If this graph is to present the actual conditions in the field pretty closely, the division of the line X should be based on the scale of cotangents. In order to avoid that, in Fig. 8 the line X has been divided into units equal to the height of the trees. A clear majority of the nests were situated at such a distance from the growth that it did not exceed the fourfold height of the trees. To demonstrate the ethological differences in relation to the Skylark nesting in the same areas, I measured the angle and the distance of the nest from the forest also for this species. The angle never appeared to exceed 10°.

The Skylarks built their nests as far as possible from high trees, farther than their sixfold height. Thus, they laid down their nests in the middle of the occupied area, if it was situated in the neighbourhood of low forest plantations. They did not nest in clearings surrounded with high trees, but appeared where there was a young plantation on one side of the felling area. On the other hand, as will be seen from Figs. 7 and 8, the Woodlark nests inside wooded areas in extreme cases. Its adaptation to environment, therefore, shows more plasticity.

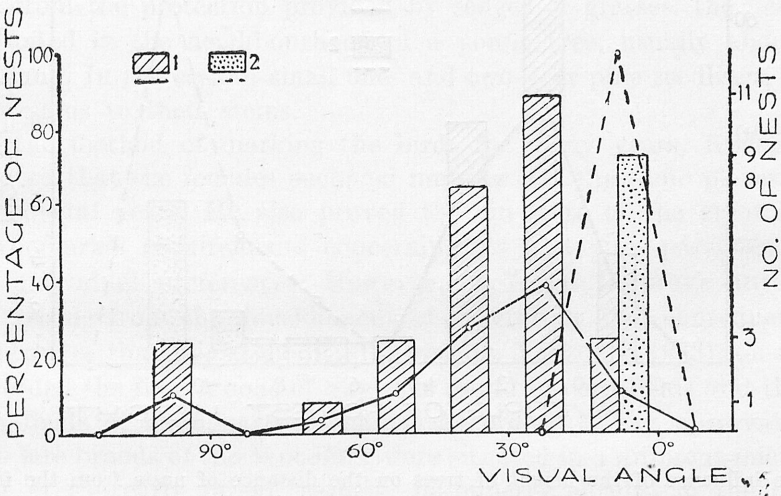


Fig. 7. The distribution of nests in a plantation with reference to the visual angle of the forest wall for the Woodlark's (1) and Skylark's (2) nests. The blocks illustrate the number of nests in the group and the lines their percentage share

The Woodlark has inhabited felling areas grown over by young vegetation for hundreds of years, whereas the Skylark, according to Makatsch (1965), began to nest in this environment scarcely several dozen years ago. Consequently, we may suppose that in the future the Skylark will oust the Woodlark from the clearings, and this last species, owing to its faculty for adaptation, will penetrate farther and farther into wooded areas.

In a considerable number of cases the nesting area lies within the boundaries of the feeding grounds, but some nests are situated beyond them. Out of the 31 nests observed, 3 represented this group: nest No. 11 in a young pine growth 20 m. from the territory proper, nest No. 13 in a timber forest 8 m. from the edge of a young plantation occupied as the territory, and nest No. 27 at a distance of about 27 m.

The pairs nesting outside their feeding grounds confined their activities at the nesting site to the building of nests, incubation, and feeding of the young. The male of such a pair only saw the incubating female to the nest. It also came flying to entice the female from the nest and next fed the nestlings.

Otherwise it stayed in the feeding grounds away from the nest. The female, having left the nest, immediately followed the male to the feeding grounds, where it fed and trimmed its feathers. The nests of this kind were, however, built under exceptional circumstances, after the destruction of the original nests.

The nearness of trees which might serve as observation posts has also a bearing upon the choice of nest sites. Planting twice as high pines in some places of a plantation, I tried to exert influence on the choice of the birds.

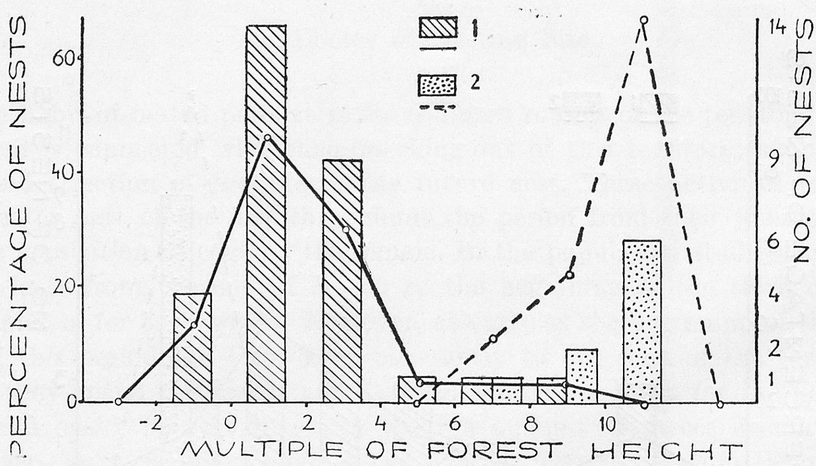


Fig. 8. The influence of the height of trees on the distance of nests from the forest edge, expressed by the multiples of the tree height for the Woodlark (1) and Skylark (2)

The experiment came off until the timber forest had been cut down. In wooded areas the nearness of a timber forest is, therefore, of greater importance than the close neighbourhood of observation trees.

The last indispensable condition of choice is an open stretch round the site. In old plantations the presence of paths or even frequented roads has a positive effect in this respect. They evidently play a part of a run, the need of which has been emphasized by many ornithologists (Koffán, 1960; Sokołowski, 1936; Witherby et al., 1948). Half the nests examined were less than 8 m. from an open area. Thus, roads are often a factor determining the position of nests. Moreover, they are a place where Woodlarks feed and display most intensely, or a favourite part of the occupied territory.

Early in the spring in the pine plantations covered by the present investigation the Woodlark has only a few plants at choice such as might afford shelter for its nest. *Carex ericetorum* prevails in such plantations, *Festuca ovina* being dominant in poorer plantations and other grasses *(Gramineae)* in wooded areas, once cultivated fields. On arrival, the female finds, in addition to the young pines, clumps of last year's grasses, in which it might hide its nest. As a result, most of the nests examined (55%, N = 29) were situated under

grasses or under tufts of sedge (31%). Two nests were placed away from any possible herbal shelter, one under a twig of a young pine, 20 cm. in height, and the other in a clump of one-year shoots of a hornbeam. Two nests were found in clumps of *Vaccinium myrtillus* (cf. Table II). It should, however, be emphasized that where the sedge is present in plantations, the Woodlark preferably builds its nest under it, for the sedge is a suitable plant and its stiff leaves are well fitted for affording cover. Its tufts grow in the bends of furrows ploughed during afforestation and form a kind of eaves, up to 10 cm. high, completely intercepting the view of the nest from above.

Apart from the protection provided by sedges or grasses, the nest was as a rule situated in the neighbourhood of a young tree, usually about 15 cm. from its trunk. In the case of small one- and two-year pine seedlings, the nests were contiguous to their stems.

Using the method of marking the birds for many years, KOFFÁN (1960) demonstrated that the females occupied more or less the same places for their nests for several years. He also proved that in spite of the great plasticity of the Woodlark's requirements concerning its nest site, particular females show no individual preferences. However, he failed to prove any seasonal variation arising from the development of vegetation and, consequently, any biotopic changes that might modify the results. PÄTZOLD (1963), on the other hand, recorded the first broods of Skylarks found in corn-fields and the second broods in fields of papilonaceous plants. According to my observations, the nests with late broods of the Woodlark were situated in a different microhabitat from that of the early brood, namely, in bilberry shrubs, in the middle of plantations, and in timber forests, which seems to correspond with the data published by PÄTZOLD (1963).

KOFFÁN (1960) described two nests situated outside the feeding grounds, one 100 m. and the other as far as 200 m. from them. Similar findings have been presented by HARRISON and FORSTER (1959).

In DELIUS'S (1963) opinion, Skylarks build their nests in places conspicuous by dense vegetation, which disagrees with PÄTZOLD'S (1963) view. In pine plantations the nests of Woodlarks were sooner built in places where there was less vegetation, which fact became more evident with the age of the plantation and is in keeping with SOKOŁOWSKI'S (1958) opinion. This may also be connected with the anatomic structure of this lark, whose longer tail enables it to take to the air and to alight more vertically.

2. Making of Holes in the Ground

The Woodlark starts building its nest with scraping out a hollow in the soil. It took a long time to prove that this bird does not place the nest in natural depressions of the ground, but in scrapes that it has prepared itself. Not only REY (1905), but still KRAMPITZ (1952) claimed that the depressions are of natural origin, whereas WITHERBY et al. (1948) and VOLCHANECKY (1954)

passed over this question. NIETHAMMER (1937) and GEUROUDET (1954) wrote that the hollows are made by the birds, in which they were supported by WADEWITZ (1957) and LABITTE (1958). KOFFÁN (1960) dealt with this matter more closely.

The late discovery of the proceedings of Woodlarks was caused by the fact that they keep quiet at work and are difficult to perceive against the background of the surrounding vegetation. The preparation of hollows concludes the period in which the birds make their rounds of the territory. On account of the above-mentioned difficulties I managed to gather only scanty observations, which are as follows:

A pair of Woodlarks that had occupied an area since April 2, 1964 began to make hollows as late as April 12. After waking up at 5·30, both the male and female were busy exploring the area and every now and then they flew over to their feeding ground till 9·30. Then they started to dig out hollows, working silently and secretly. The birds disappeared alternately in the same clump of plants to turn up after a while but, having taken a short walk, they resumed their work again. They stopped working at 11·35. Then I examined the place carefully and found 2 new hollows, 8 m. apart and 38 m. from the spot where they had spent the preceding night. The hollows were both situated under tufts of sedge; one was shallow and at a distance of 20 cm. from a young pine and the other was much deeper and well-hidden under the twigs of a four-year pine. On the next day (April 13) one of the hollows was left untouched, whereas the other one was deepened in spite of the rainy weather. Nevertheless, the nest was placed in a new hollow, prepared later 40 m. from them and only 10 m. from the roost. After a month, on May 12, six-day nestlings were found in this nest. It follows that the first egg was laid 6 days after my watching the birds on April 13.

On the same day (April 13) I saw another pair make 2 hollows and these birds commenced to build a nest four days later. They took 3 days to complete the work and on the last day the female laid an egg (April 21). Thus, 7 days passed from the completion of the hollow to the laying of the first egg.

The male and female keep quiet in the neighbourhood of the hollow and do not utter alarm notes less than 20—40 m. from it.

The preparation of several hollows, most frequently 2—4, by each pair is the rule. The hollows are usually disposed irregularly in twos, in which they lie near each other (5—10 m.). This is undoubtedly due to the fact that either bird makes a separate hollow.

In nearly all cases the hollow was surrounded with a mound of earth, visible on the side opposite to the tuft of plants under which it had been dug out and where the earth was inconspicuous among the leaves. The amount of earth round the hollow is, however, very small as compared with its size.

The shape of hollows was fairly uniform owing to the similarity of the substratum (loose sandy soil with a small admixture of clay). The hollow was a paraboloidal depression, often asymmetrical, with its vertex displaced towards

the tussock of grass under which it was situated. The greater steepness of the wall on one side was caused by the presence of roots which had withstood the scraping of the birds. The horizontal projection of a hollow is an oval, the long axis of which is parallel to the entrance. In more compact soils the hollows were widened in the upper part (Fig. 9). The measurements of 11 complete hollows, in which I found nests later, were as follows: the diameter parallel to the entrance ranged from 95 to 120 mm., averaging 110 mm., the diameter perpendicular to the entrance was from 73 to 127 mm., on the average 104·3 mm., and the depth varied between 34 and 73 mm., with an average of 54·6 mm. Similar shapes and measurements were found in the hollows formed not in the ground but in putrefying leaves of hornbeam or oak.

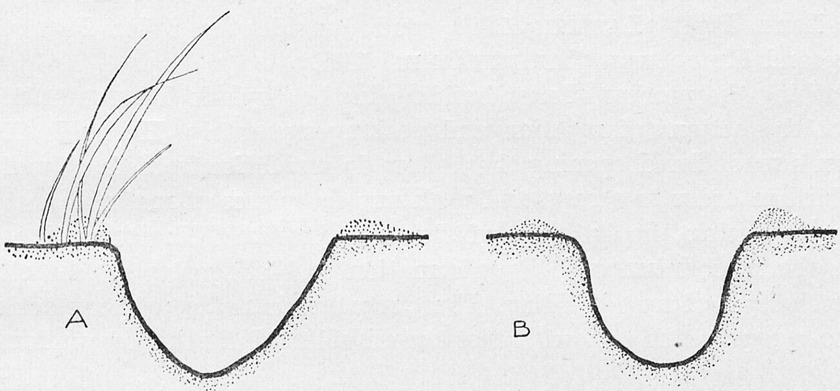


Fig. 9. Shapes of hollows scraped out by Woodlarks in loose (A) and compact (B) substrata

The male and female worked at the formation of their hollows chiefly in the morning. The rate of digging was different. One female took 2 days to dig out a hollows, another only 1 day.

The female chooses a hollow for the nest much later, after its nest building instinct has developed. This explains the behaviour of one of the pairs observed, which made three hollows before building its nest in the fourth one.

As I have already mentioned, out of the authors dealing with the biology of the Woodlark, Koffán (1960) gives most attention to the problem of hollows. However, his results are not always consistent with the observations presented above. According to Koffán, in Hungary, where this species nests twice a year, the interval between the completion of the first hollow and the laying of the first egg lasted 11 days for the first brood and half this time for the second brood. The number of hollows made by a pair reported by Koffán (o. c.) agrees with that observed by me, but I failed to find a confirmation of his statement that most hollows are 2 m. apart, which arrangement was typical of the population investigated by him, though in exceptional cases the distance between hollows reached 800 m. The measurements of hollows given for the

Hungarian population (KOFFÁN, 1960) indicate that they are markedly deeper, whereas their diameter is slightly smaller, which differences are probably connected with the nature of the substratum. KOFFÁN (o. c.) explains the scantity of earth lying round the hollow and accumulated during its formation by the fact that the birds carried it away in their bills. He calls the similar removal of objects that fell into the hollows after their completion "the caring for the hollows".

The technique of hollow building has been noted by different authors (HOFMAN, 1951; LABITTE, 1958; KOFFÁN, 1960). It consists in two actions, i.e., first the bird moves round, tripping quickly in the hollow in order to mould it, and next it pecks out earth and rootlets. As will be seen from the results of studies on other birds, the method of building is pretty uniform in all the birds that make their nests on the ground, e.g., the Skylark (DELIUS, 1963), Crested Lark, Pipit (LABITTE, 1958) and, outside the order *Passeres,* the Lapwing and Mute Swan (SCHILDMACHER, 1965).

Describing the process of nest building in the Skylark, DELIUS (1963) does not treat the actions of rotation and pecking separately. He holds that the movements made for deepening the hollow do not differ from those performed by the bird in order to scrape and peck out the pieces of material that stand in the way during the building of the nest proper. This conception better explains the mechanism of hollow formation and integrates all the elements of the technique of nest building. Thus, rotation is not a primary action but serves to scrape earth out with feet on all sides of the hollow uniformly.

3. Nest Building

When the hollows are ready, the female takes on itself the whole task of nest building, whereas the male only keeps it company. Therefore, the opinion held by many authors that the male also takes part in nest building (NETHERSOLE-THOMPSON, 1932; PORTENKO, 1954; MAKATSCH, 1965) is inexact. In the light of the present observations it is true of hollow formation only. Instead, the building of nests exclusively by females is the rule endorsed by numerous writers (ABS, 1963; DATHE, 1952; DELIUS, 1963; ENDES et al., 1967; LEBEURIER and RAPINE, 1935; LÖHRL, 1944; PICKWELL, 1942; SUTTON, 1932; WADEWITZ, 1957).

Woodlarks build new nests for each, new and repeated, brood. While building a nest the female performs four actions:

A. Gathering of material. The female gathers material for the nest in the close neighbourhood of the hollow. It chiefly tears off pieces from the last year's tufts of grass, moss, etc. In order to break off a blade of grass the female pulls at it with its bill, with its head raised high and, when this is ineffective,

it steps back energetically. I also saw it picking up detached blades scattered on the ground. The female breaks moss off by grasping at it close to the base. The bird does not let the gathered material drop, but holds it in the bill with the help of the tongue. When it has gathered a bundle, it returns to the nest. Not only the amount of material held in the bill, but also the distance from the nest is decisive in regard to the interruption of gathering. If the distance is long, the bird usually returns with a larger bundle of material.

B. Bringing of material and dropping it into the hollow. Standing by the nest, the female drops the bundle held in the bill into it, leans over it, sometimes trims something with the bill, but most often moves away immediately. My observations show that the Woodlark brings nest material both on foot and flying. For example, one of the nests, the construction of which I watched closely, was situated in an old felling site, 20 acres in area, adjacent to a pine plantation, from where the female fairly often flew carrying material and alighted about 6 m. from the nest. When it collected nest material in the felling area, it brought it coming on foot. Koffán (1960) claimed that the females bring material almost exclusively on foot, whereas Krampitz (1952) observed them carrying it in flight. Topographical conditions supposedly play an essential part in this respect.

C. Treading down combined with rotation. When shaping the nest, the female turns round in it, crouching low every now and then. It gets into the nest, squats, and performs half a turn, with its head directed towards the entrance. Then it turns round once or twice, stops at various moments, and presses its body deep in. At this operation the bird hides its neck in the nest and touches the edge of the nest with its upturned bill. Unlike the front of the body, its back (tail and remiges) is raised upwards. The whole body trembles owing to rapid movements of the legs treading down the bottom of the nest, whereas the body weight rests on the breast. This is the way the bird dishes the nest cup.

The hollow with nest material dropped into it in a disorderly manner is difficult to distinguish from its surroundings. The hand of rotation is arbitrary, both when the bird performs only half turns (180°) and when the turns are full (360°). Observations made on particular days showed the casual predomination of either direction. The female treads 1—5 times, for the most part 2—3 times, during a single revolution. It treads down the posterior part of the nest most; hence most of the nests observed had their back wall overhanging and the front wall flattened. This technique of construction explains the mode of formation of the nest with a roof reported by Ash (1951).

D. Arranging of material with the bill. The above-mentioned operations are not sufficient to put some particularly long blades in order and, for this reason, the female occasionally adjusts the hindering pieces of material with the help of its bill. It then bends its head down and the tail is raised vertically.

During incubation it assumes a similar posture, when turning the eggs and pecking out parasites.

The duration of nest building is very variable. Female No. 15 built its nest for 5 days (Fig. 10). On the 6th day, when it had laid the first egg, it still brought some building material. On the other hand, female No. 24, having completed the nest, left it untouched for 3 days, before it laid the first egg.

The female began building after the sunrise, every day later (e.g., 40, 57,

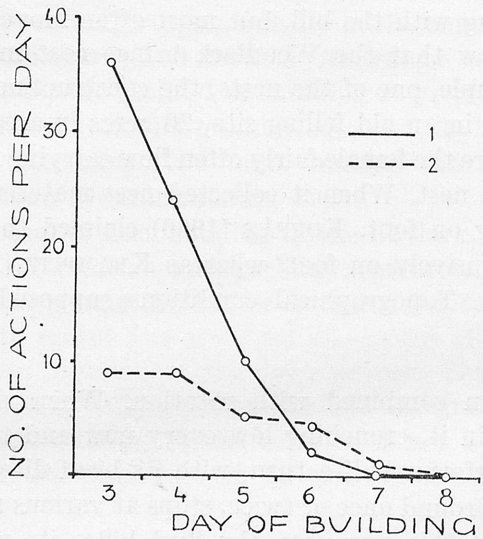


Fig. 10. Intensity of Woodlark nest building on successive days of work. 1 — number of the droppings of material by the bird into the nest, 2 — number of the gettings of the bird on the nest to mould the material (based on the data from one nest)

and 97 minutes after the sunrise). It also worked shorter but more efficiently (Table VIII). Nest building was limited to the morning hours.

On the consecutive days of building the average interval between particular returns of the bird with material to the nest diminished from 6·7 minutes to 3·9 minutes and the intervals between its mountings on the nest from 27·6 minutes to 7·8 minutes. The female built the nest most dilligently in the first hour of the first day of observation, i.e., it brought material 22 times in an hour. In the first hour of day, i.e., at 5 a.m., the work proceeded most efficiently, afterwards its intensity diminished gradually to zero. On the 5th day the cloudy weather retarded the commencement of work by an hour (6·00). The activity rhythm on the particular days of nest building (from the 3rd to 7th) is presented in Fig. 11.

The male kept the female company during work, but only once, towards the end of building, brought a blade of dead grass, which its mate wove into

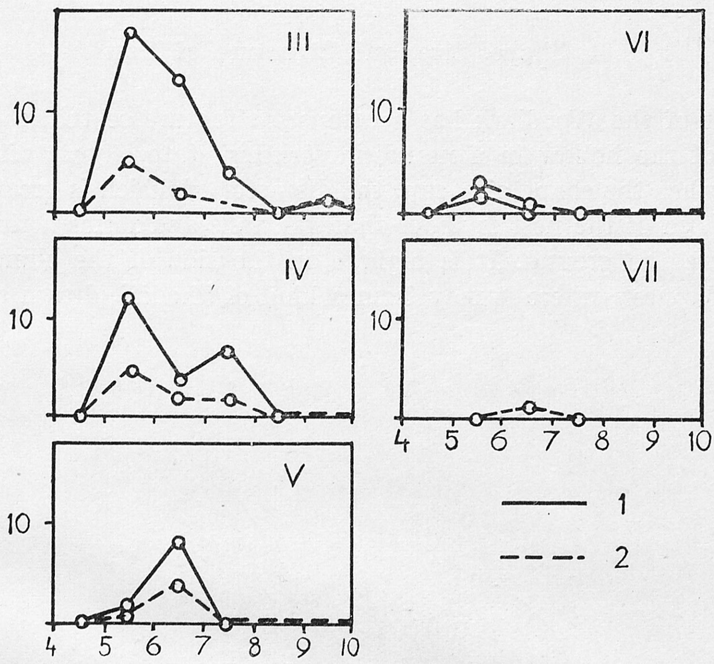


Fig. 11. The course of Woodlark nest building on successive days of work (based on the data from the same nest as in Fig. 10). The number of actions per hour is given on the ordinates, the hours of day on the abscissae. 1 — number of the droppings of material by the bird into the nest, 2 — number of its gettings on the nest to mould it. The Roman numerals indicate the number of the day counting from the commencement of hollow-formation (the 1st egg laid on the 6th day, the 2nd on the 7th)

Table VIII

Intensity of Work of a Female Woodlark on 3rd—5th Days of Nest Building
(I carried out no observations on the 1st and 2nd days of building lest I should frighten the bird away)

Day of Building	How Many Minutes after Sunrise Work Was Started	How Long the Bird Worked, in Minutes per Day	How Many Times the Bird Brought Material to the Nest	How Many Times the Bird Brought Material to the Nest in Hour	How Many Times the Bird Got On the Nest and Tread It Down	How Many Times the Bird Got On the Nest in an Hour
3rd	40	248	37	9·0	9	2·2
4th	52	123	23	11·2	9	4·4
5th	97	39	10	15·4	5	7·7

the nest. On the second day of incubation of the full clutch by the female the male also brought a rootlet and left it by the nest.

Koffán (1960) writes that the females observed by him built nests on the average for 2—4 days, though they could have completed their work in one day. He, too, reports an interval between the completion of the nest and the laying of eggs, and so do some other authors (Abs, 1963; Labitte, 1958).

4. Shape, Size, and Structure of Nest

The nest of the Woodlark has a compact structure so that it can still be taken out of the hollow in a non-disintegrating state a year after building. It generally has the shape of a cup, the diameter of which is greater than the depth. The rim of the nest is wider than its walls and forms a threshold projecting above the ground. It is highest on the side of the clump of plants sheltering the nest, where it may form a kind of "hood", drawn slightly over

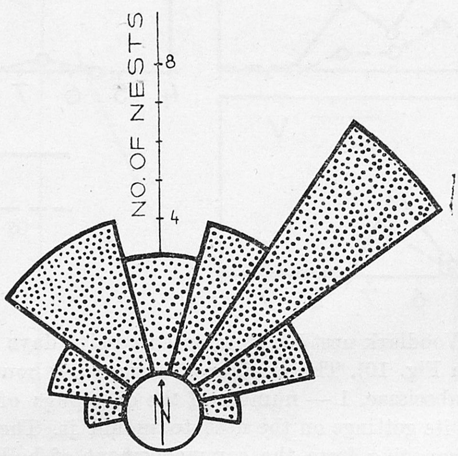


Fig. 12. Entrance orientation with regard to the points of compass in 30 nests of Woodlarks

the nest. It arises owing to the fact that the tuft of plants prevents the bird from pressing the material in properly. The edge of the nest is also lowered at theentrance on the opposite side by the repeated entries of the bird into it. Each nest has as a rule one such entrance. Only one nest, situated in a thicket of bilberries, constituted an exception and had two entrances, one for the male and the other for the female. The entrances of the 30 nests examined were for the most part turned to the points of the compass ranging between the north-east and north-west, as presented in Fig. 12. A majority of the nests had the north-east exposure (27 %).

The inside of the nest is a slightly elongated cup with its dimensions averaging 66·1 by 61·7 mm. and the long axis oriented to the entrance. The average depth is 52·3 mm. The mean values have been calculated from the measurements of 10 fresh nests. As the nests are used, their depth becomes smaller and diameters increase. The change in the shape is the greater, the more nestlings are in the nest, and the nest-cup with a brood of 5 may even measure 110 × ×100 ×25 mm. The thickness of walls is on the average 26·6 mm.

Although the nest constitutes a uniform whole, three layers may be distinguished in it. Only two layers have hitherto been mentioned in ornithological

literature, the lower fundamental layer and the upper one. A close analysis of a large number of nests reveals the occurrence of 3 layers, a fundamental, a structural, and a lining.

The fundamental layer is characterized by its thick materials. Functionally, the rim of the nest, running round the edge of the hollow, must be included in this layer, for it contains most moss, protecting the nest from getting wet and brought together with the material of the fundamental layer in the first stage of building. The material of this layer in the nests examined consisted

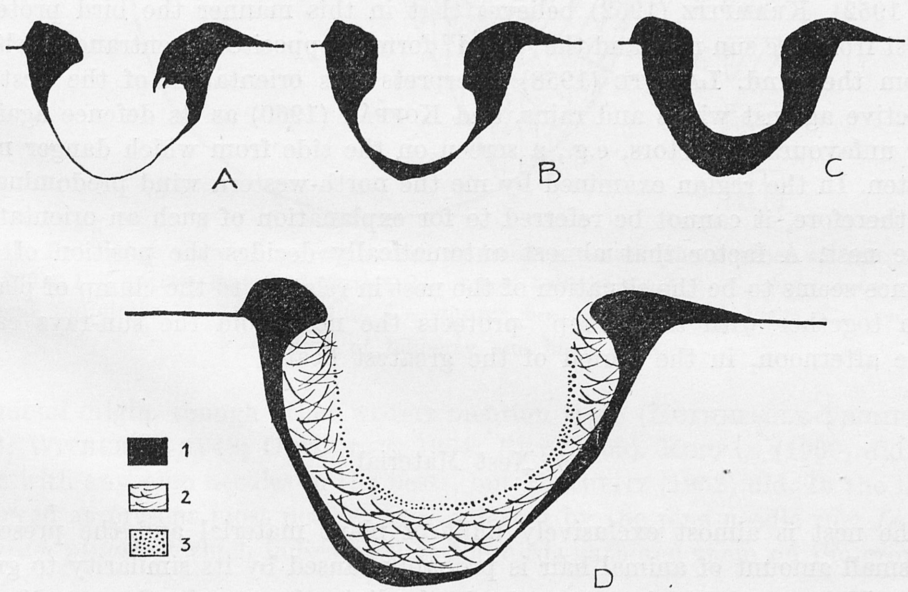


Fig. 13. Successive stages of nest building (A—C) and the arrangement of layers in the complete nest (D): 1 — fundamental, 2 — structural, 3 — lining

of hard pieces of stems, dry grass, stalks and inflorescences of herbs, leaves of bilberry, pine needles, and mosses of the genera *Hypnum* and *Polytrichum*.

The main, structural layer of the nest is built of dry blades and soft bents of grasses. Owing to the technique of treading, the wedge-like bundles of material overlap each other compactly to form a uniform structure. This layer comprises about 70% of the total nest material. It may also contain some elements of the fundamental layer (moss, pieces of pine needles).

The lining layer is the thinnest and constitutes scarcely 5% of the whole nest or even less. In the walls it is thicker and more evident than in the bottom, though in some nests it is hardly visible. It is difficult to isolate this layer from the rest of the nest, but it differs from this last essentially in material, being composed almost exclusively of delicate rootlets, which are absent from the preceding layers. Hair may also be found in it. Since it does not differ

from the rest of the nest in colour and is hardly visible from above, other authors have not distinguished it.

Owing to the technique of treading applied by the female, it builds the top part of the nest earlier than its bottom, and the incomplete nest resembles an inkpot with its walls undercut and almost without the floor (Fig. 13). It is only when the sides have partly been made that the female proceeds to build the bottom (at the beginning of the second day) alternately with the walls.

The situation of the entrance on the northern or north-eastern side of the nest was observed in most cases also by other authors (Koffán, 1960; Krampitz, 1952). Krampitz (1952) believes that in this manner the bird protects its nest from the sun-rays and the "hood" formed opposite the entrance shelters it from the wind. Labitte (1958) interprets this orientation of the nest as protective against winds and rains, and Koffán (1960) as its defence against other unfavourable factors, e.g., a screen on the side from which danger may threaten. In the region examined by me the north-western wind predominates and, therefore, it cannot be referred to for explanation of such an orientation of the nest. A factor that almost automatically decides the position of the entrance seems to be the situation of the nest in relation to the clump of plants which together with the "hoop" protects the nest from the sun-rays early in the afternoon, in the period of the greatest heat.

5. Nest Material

The nest is almost exclusively built of plant material and the presence of a small amount of animal hair is probably caused by its similarity to grass blades. Hair was found in two nests, in the lining layer only. In nest No. 15 there was a bundle of some dozen hairs of the roe deer and in nest No. 11 two horse hairs, about 30 cm. long.

The results of a quantitative analysis of materials used to build a nest are presented in the form of a diagram in Fig. 14. The nest used for this analysis had 2,391 parts, of which narrow leaves of grasses formed 57·9%, mosses *(Polytrichum* and *Hypnum)* 11·3%, pine needles 7·0%, soft bents of grasses 5·8%, leaves of broad grasses and billberry 5·3%, rootlets 5·1%, hard stems 4·6%, and whole tufts of grass with root necks. The percentage values were calculated from the numbers of particular elements, for weight or voluminous proportions would change relations between them. As the female must bend down to pick each particle separately, irrespective of its weight or volume, I adopted the method of counting the number of particular kinds of materials as justified. A general analysis showed that last year's grasses are the main nest material.

Koffán (1960), Krampitz (1952) and Sokołowski (1936, 1958) also write that the main material of the Woodlark's nest consists of last year's grasses. However, Krampitz (1952) and Koffán (1960) did not find any materials

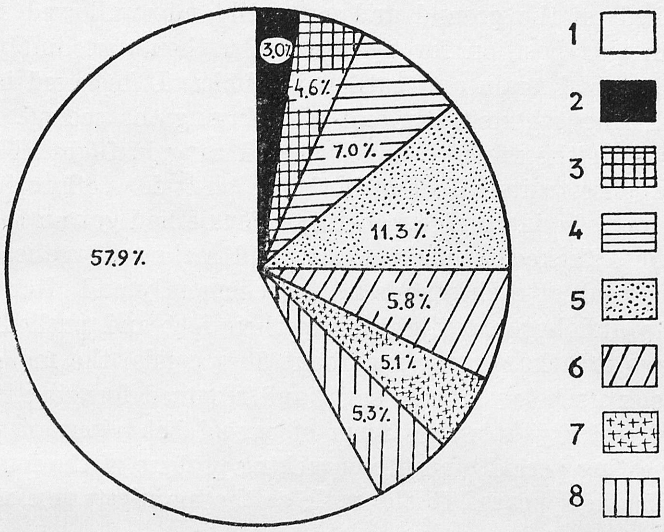


Fig. 14. Percentage share of materials used to build one nest (the number of parts used N = 2391). 1 — narrow leaves of grasses, 2 — whole tufts of grass, 3 — hard woody pieces of stems and stalks, 4 — pine needles, 5 — mosses, 6 — pieces of soft bents, 7 — rootlets, 8 — leaves of billberry and broad grasses

of animal origin, though other writers mention them (NETHERSOLE-THOMPSON, 1932; WITHERBY, 1948; GEROUDET, 1954; REY, 1905). KOFFÁN (1960) did not meet with any pine needles in the nests, but KRAMPITZ (1952) did. In the nests observed at present most needles were infested by the pine needle rust *Lophodermium pinastri*, which indicates that the birds gathered them on the ground.

IX. EGGS

1. The Laying of Eggs

Just before laying an egg the female enters the nest and, as in the period of building, alters something in its construction with the bill. In the end it settles itself quietly and keeps motionless. Before laying the first egg it often leaves the nest for a while. One of the females observed entered and left the nest as many as 5 times, whereas it laid the next eggs the first time it seated itself in the nest.

In the case of one clutch I managed to measure the time the female stayed in the nest before laying particular eggs. The time was 27 minutes for the first egg and 80 minutes for the next ones. All the eggs were laid in the morning, from 6·18 to 9·45, at nearly 24-hour intervals.

One of my collaborators, Mr. A. SACHANBIŃSKI, observed interesting behaviour of a female Woodlark in connection with egg laying. Having left the

nest, it crouched on the ground and gathered and swallowed small pebbles. It remained in this position for 2—3 seconds, then rose and, having taken a few steps, crouched again and gathered pebbles. It behaved in this fashion twice, before laying the first egg and after laying the second. At that time the male stayed in the vicinity, it called and sang in flight. The female left the nest in response to its calls and both the birds flew off to forage. On the first day of the egg-laying period, when the female had got on the nest several times, the male attacked it unexpectedly and rather energetically. Next the birds started to peck at each other's heads vehemently and after a few seconds they sprang up and began to fight using their feet and pushed against each other. After two attacks, lasting for about 30 seconds, the male flew off and the female shook itself, as after a bath, and resumed foraging interrupted by the fight. Undoubtedly, it was a form of sexual behaviour of the male, left after the pre-nesting period, and the crouching posture of the female preceding the fight may have appeared to the male as the manifestation of its readiness to copulate.

When the female was laying the fourth egg, the male even approached the nest, made the female leave it, and peeped into it to move away after 2 seconds. This was a sign that the male's instinct of feeding the young was beginning to rouse.

The clutch size of the Rzepin population of Woodlarks ranges from 2 to 6 eggs, averaging 3·97 (Table IX).

Table IX

Clutch Size in the Woodlark Population of the Rzepin Region

Clutch size (No. of eggs)	2	3	4	5	6
No. of nests	2	7	9	8	1

The late clutches are larger even in the case of the same female. For example, female No. 6 incubated 3 eggs, but when they had been destroyed, it laid 5 eggs in its new nest. In May the size of 18 clutches examined averaged 3·78, towards the end of May and at the beginning of June 4 clutches consisted on the average of 5·25 eggs each, and at the end of June 3 clutches of 5 eggs each (Phot. 3).

Delius (1963) observed similar behaviour of a female Skylark, which got off the nest after laying an egg and crouched motionless on the ground. The laying of more eggs in later clutches agrees with the statement of Lack (after Haartman, 1954), according to whom the fact that longer days bring about larger clutches is a general regularity.

2. Size and Colour of Eggs

A total of 35 eggs from 12 clutches were measured in order to obtain the egg size characteristic of the Woodlark population under study. The length of eggs ranged between 18·7 and 22·5 mm., averaging 20·63 mm. and the width was between 14·5 and 16·8 mm., on the average 15·77 mm. The largest egg was 21·9 ×16·8 mm. and the smallest 20·6 ×14·5 mm.

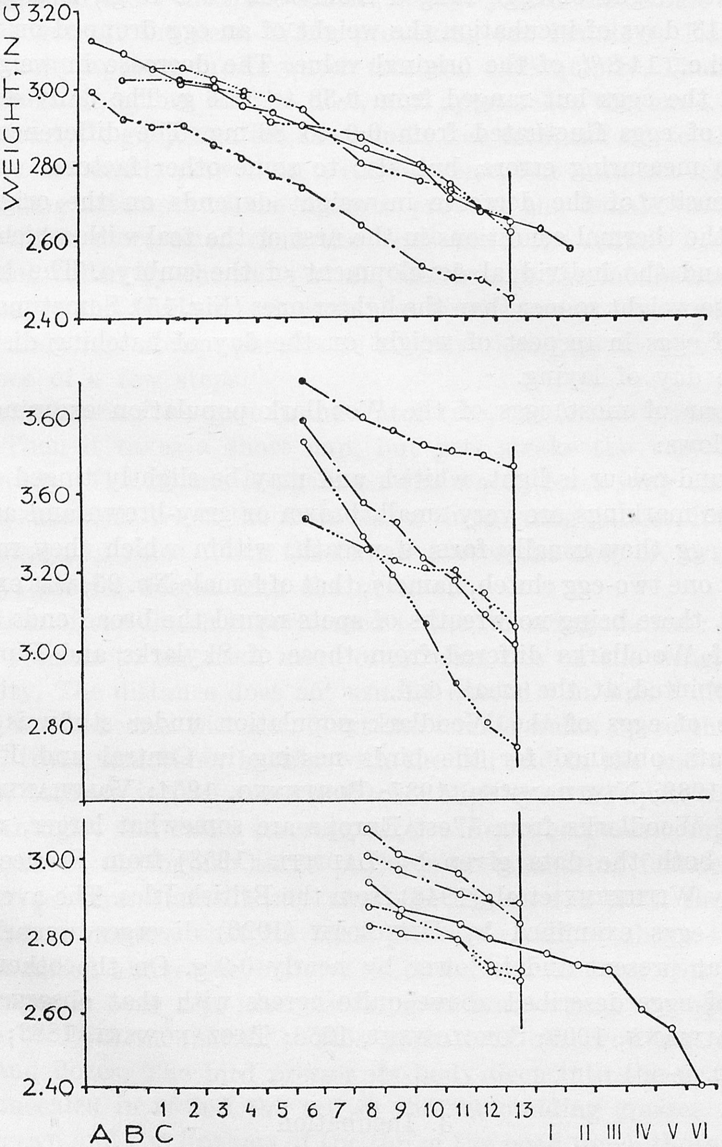


Fig. 15. Decrease in the weight of eggs on successive days of incubation, observed at the same time in 3 Woodlark nests (May 1964). A, B, C — days of egg-laying; 1, 2, 3 ... 13 — days of incubation; I—VI -- days of nestling stage. The solid lines represent addle eggs

Eggs laid by the same female resembled each other in size and shape. Repeated clutches outsized the early ones. In female No. 6 the average for the first clutch was 21·00×16·34 mm. and that for the second clutch 21·85×16·77 mm. Thus, the second clutch not only consists of a larger number of eggs but also their volume has increased. On the day of laying the weight of eggs ranged within wide limits, from 2·99 to 4·0 g. The average weight from 21 eggs was 3·38 g. on the first day of incubation. On the last day before hatching the weight of eggs ranged from 2·62 to 3·45 g., averaging 2·88 g. During the 13 days of incubation the weight of an egg dropped on the average by 0·50 g., i.e., 14·8% of the original value. The decrease in weight was not equal in all the eggs but ranged from 0·38 to 1·36 g. The daily decrement in the weight of eggs fluctuated from 0·0 to 80 mg. The differences were not only due to measuring errors, but also to some other factors.

The intensity of the decrease in weight depends on the original weight of the egg, the thermal conditions in the nest or the zeal with which the female incubates, and the individual development of the embryo. The heavier eggs generally lose weight sooner than the lighter ones (Fig. 15). Sometimes, however, the order of eggs in respect of weight on the day of hatching disagrees with that on the day of laying.

The colour of most eggs of the Woodlark population examined presents itself as follows:

The ground-colour is light, whitish and may be slightly tinged with brown or olive. The markings are very small, brown or gray-brown and at the broad end of the egg they usually form a wreath, within which they may be confluent. Only one two-egg clutch, namely, that of female No. 23, was exceptionally dark brown, there being no wreaths of spots round the broad ends of the eggs. The eggs of Woodlarks differed from those of Skylarks and Pipits in their being less pointed at the small end.

The size of eggs of the Woodlark population under study is in keeping with the data obtained for the birds nesting in Central and East Europe (Donchev, 1963; Niethammer, 1937; Portenko, 1954; Volchanecky, 1954). The eggs of Woodlarks from West Europe are somewhat larger, which is indicated by both the data given by Labitte (1958) from France and those presented by Witherby et al. (1948) from the British Isles. The average weight of new-laid eggs examined by Heinroth (1926) diverges remarkably from that given at present and is lower by nearly 0·9 g. On the other hand, the coloration of eggs described above quite agrees with that observed by other authors (Naumann, 1900; Sokołowski, 1958; Taczanowski, 1882; Witherby et al., 1948).

3. Incubation

A. Behaviour of Incubating Female. In Woodlarks, as in all other *Alaudidae*, incubation is performed by the female alone, whereas the male accompanies it while feeding and next during its return to the nest. Besides, the male usually

gives the signal for the female to break incubation and is on guard, when the female has got off the nest. Thus, for example, out of the 99 cases observed in which one of the females left the nest, 76 times it was stimulated to do that by the calls of the male. As to the remaining 23 cases, I failed to establish whether its getting off the nest was caused by the arrival of the male, for the females noticed it much earlier than the observer did, and therefore its behaviour may have been induced by the sudden though silent appearance of the male. In such cases the male almost always joined the female immediately after it had got off the nest. When provoking the female to leave the nest, the male usually appears in the watch tree and calls quietly. Then, the female becomes animated, comes off the nest, and approaches the male. If the male calls it too early, e.g., just after the female has returned on to the nest, this last becomes animated, answers in a calling voice, but does not leave the nest. Such unavailing attempts of the male to provoke the female to come off the nest occur much more often than the cases when the female leaves the nest without being called by the male at all. Besides, in the incubation period the male rummages the territory, sings in the air, but most often perches in the watch tree and sings abrupt phrases so silently that they are scarcely audible at a distance of a few steps.

Seeing and hearing the male in the watch tree, the female becomes evidently reassured. Then it takes a short nap, but gets awake the very moment the male flies away. The female is again on the watch for a long time before its anxiety has subsided. When the male sees a threatening danger, it gives signals in a sharp warning voice. Then the female leaves the nest or, if the male has flown away, presses deeper into the nest.

Incubation of the clutch is performed in the following manner: after feeding the female returns to the nest, more often than not on the wing, and alights in its vicinity. The distance does not usually exceed 6 m. and I often observed it alighting much nearer the nest. Next the female walks up to the nest, stops at its edge, trims something hastily with the bill and in the end settles down. After a few seconds it performs a half-turn, slightly lifting up its wings and tail, puffs out strongly, and raises its crest, after which it becomes completely quiet.

I managed to distinguish three postures of incubating females:

"Initial" posture. Immediately after getting on the nest, the female sits down in such a manner that its back protrudes visibly above the nest and the head is raised above the body. The bird often assumes this posture also when a danger is over and after awaking or rearranging the eggs, etc.

Posture of "full incubation". This posture is observed when the female feels safe and dozes. The bird presses its body deep into the nest so that its trunk is concealed in it and the tail in the surrounding grasses. The head is then withdrawn and the feathers of the top of the head touch those of the back. In this posture the female is difficult to notice even for someone standing near the nest (Phot. 4). It also assumes a similar posture when threatened with sudden danger it cannot leave the nest imperceptibly.

Posture of "anxiety". In this posture the female thrusts its head far to the front and obliquely upwards and looks round intently, turning the head simultaneously (cf. Phot. 5). The bird usually assumes this posture just before leaving the nest.

During the day the female often takes a short nap, which may last from 3 seconds to a minute and a half. The dozing female has its head withdrawn but not turned backward as during normal sleep. It very rarely sleeps with the head hidden among the shoulder feathers in the daytime, which I observed only twice.

The rate of respiration of incubating females ranges from 67 to 88 per minute at Mo equal to 80.

The rearrangement of eggs is always preceded by a careful examination of the surroundings. The sequence of actions is kept so strictly that, whenever a female has been alarmed by anything, immediately after the subsidence of its anxiety it becomes interested in the arrangement of the eggs and begins to turn them over. Thus, a loud noise of a tractor, an alarm call of the male, or the flight of a Jay (Phot. 6) stimulated the female to alter the egg arrangement. First it looks round intently, rises, moves back and, with its feet resting against the posterior edge of the nest, it shifts the eggs with two or three movements of its head. In doing this the female often turns back, which releases its full rotary movement round the nest axis (Fig. 16).

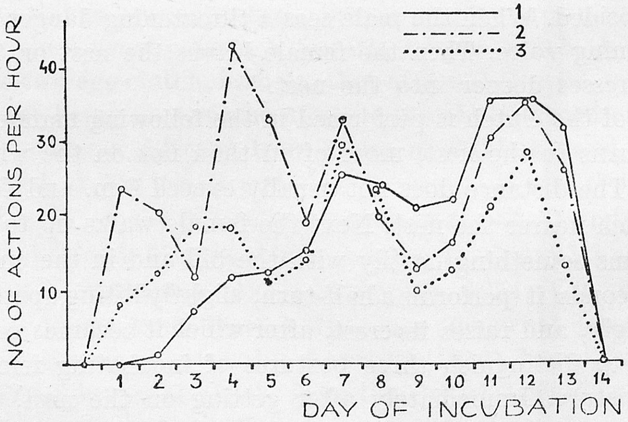


Fig. 16. Actions performed by incubating female on the nest on successive days of incubation. 1 — removal of parasites and greasing of feathers, 2 — rearrangement of eggs, 3 — moulding of nest by turning round and treading down the edge. (Note: the word HOUR at the vertical axis of the graph is to be replaced by the word DAY)

It will be seen from the graphs in Figure 16 that the frequency with which the female rearranges the eggs varies fairly markedly on particular days. On the average the bird does it 4 times in nearly 100 minutes of incubation. The first time it usually rearranges the eggs 10 minutes after getting on the nest and repeats the action after further 20 minutes and next every half an hour.

While incubating, the female continues shaping the inside of the nest. There being only one entrance, the female must perform half a turn in the nest. This action is repeated more than 10 times a day (about 150 times throughout the incubation period), which undoubtedly has an effect on the smoothness of the walls and the shape of the nest. The bird retains its nest-building instinct till the end of the incubation period.

The frequency of actions connected with keeping the plumage clean, greasing the feathers and removing parasites (Phot. 7) varies during incubation. In the first days the female trims the plumage and cleans it outside the nest, often on the ground or in a tree. Since the number of parasites in the nest increases gradually, the bird must eventually perform these operations also on the nest. As the term of hatching comes nearer, the bird repeats them more and more often (Fig. 16), and in the end it tidies up every 40 minutes.

The incubating female is on the watch for danger, looks about, or watches the singing male. In the morning or after the rain it drinks dew and rain drops off the surrounding grass blades without interrupting incubation. However, the female rushes out of the nest for a while to catch insects (e.g., ants) passing by near the nest.

The female Woodlark is a close sitter, owing to which it avoids most dangers. While combing the area, one may pass by the nest at a distance shorter than 1 m. without flushing the female. On the 6th day of incubation female No. 27 did not leave the nest when twigs were broken 20 cm. above its head. Neither did the touching of the bill of female No. 12 induce it to run away (Phot. 8). Therefore, taking photographs of females, even from a distance of 60 cm., presents no difficulties in the period of more advanced incubation. Some females

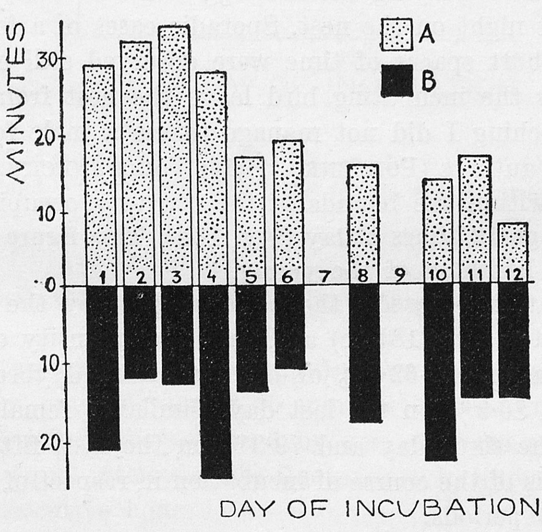


Fig. 17. Effect of the advancement of incubation on the length of absence of the female flushed from the nest by the approaching observer. A — duration of observer's visit to the nest site, B — length of absence of the female from the nest after the observer's departure

let themselves even be shifted about 2 cm. aside with a finger. They, however, get off the nest more readily when scared from behind. The flight impulse depends on many factors, and not all females behave in the same fashion. The females forced to leave the nest return to it at various intervals (Fig. 17). The periods of their absence from the nest become shorter with time, but there are individual differences in this respect.

When frightened away from the nest in the last days of incubation, the female Woodlark, like females of other species, tries to deceive by flying close to the ground and crouching on it every now and again. At the same time it flutters its wings and spreads the tail wide. In 2- or 3-year plantations they move away in this manner up to 20 m. and, if followed, still farther.

When the observer remains by the nest, the female comes down at a distance of 6—8 m. for the first time and then somewhat farther. If this manoeuvre has no effect, i.e., if the persecutor does not follow the bird, this last gives it up in 10—15 seconds.

Before leaving the nest the undisturbed female looks about for several seconds, springs on to the rim of the nest but does not take wing until it has walked away a distance of up to 200 cm. Then it flies to the calling male and together with it to the feeding ground.

A comparison shows clearly that the distances of the places from which the females rise are far shorter than those where they alight returning to the nest.

B. Intensity of Sitting throughout the Period of Incubation. The female starts incubating after laying the last egg, but it sits down on the nest at irregular intervals before laying the last egg and before laying the fourth egg it spends the first night on the nest. Sporadic cases of a female settling itself on the nest for short spaces of time were observed still earlier.

Hunger makes the incubating bird leave the nest from time to time. In spite of long watching I did not manage to see a male feeding its mate, as suggested by some authors (Portenko, 1954; Volchanecky, 1954). The female collects its food within the bounds of the territory occupied. It gets off the nest on the average 12 times a day (Fig. 18a). This figure keeps more or less strictly until the hatching of the young.

As the incubation proceeds, the periods spent by the female out of the nest become shorter (Fig. 18b, c) and thus the intensity of sitting increases. Female No. 15 incubated 62·5% of the time from daybreak to nightfall on the first day and 86·9% on the last day. Similarly, female No. 5 sat 56·6% of the time on the sixth day and 79·3% on the last, fifteenth, day.

A close analysis of the course of incubation in respect of its intensity allows a distinction of 3 periods:

The initial period begins practically at the laying of the penultimate egg and lasts approximately to the 6th day of incubation of the full clutch. Towards

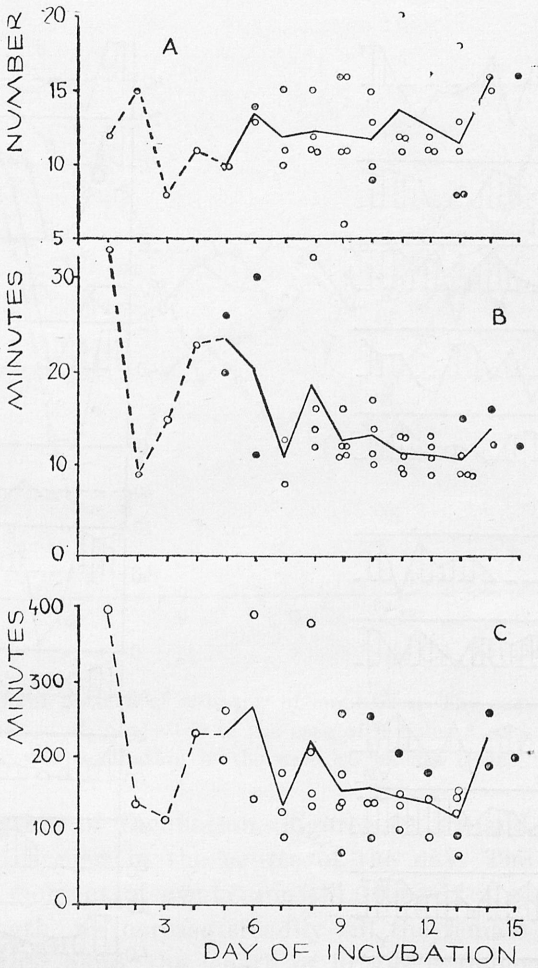


Fig. 18. Effect of the advancement of incubation on the number (A) and length (B) of intervals in brooding and on the time which the female spends away from the nest (C).

the end of this period (6th day) the breaks in sitting are still up to 177 minutes in length.

The intermediate period (7th—10th day) shows the intensity of incubation fluctuating within a range of nearly 20 minutes in consecutive hours.

The terminal period is characterized by very uniform and regular breaks in sitting at nearly equal intervals. The fluctuations in intensity do not exceed 10 minutes for consecutive hours.

Figure 19 presents the detailed results of observations carried out on the intensity of incubation on particular days, as exemplified by 2 females.

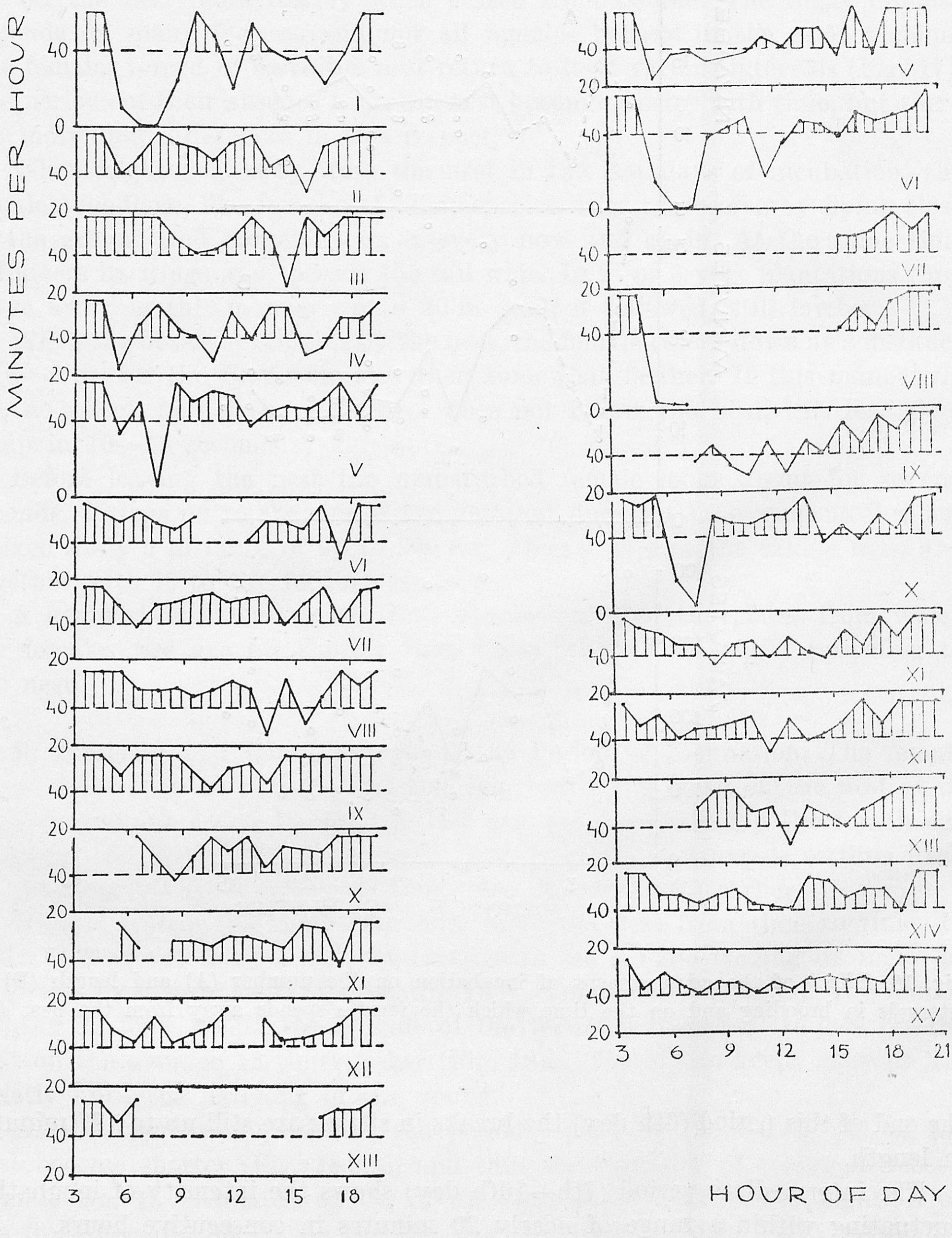


Fig. 19. Intensity of incubation of 2 female Woodlarks on consecutive days (from 1st to 13th and from 5th to 15th day, respectively). The Roman numerals indicate the successive days of incubation. If a female incubated altogether more than 40 minutes in a given hour, a suitable area has been hatched

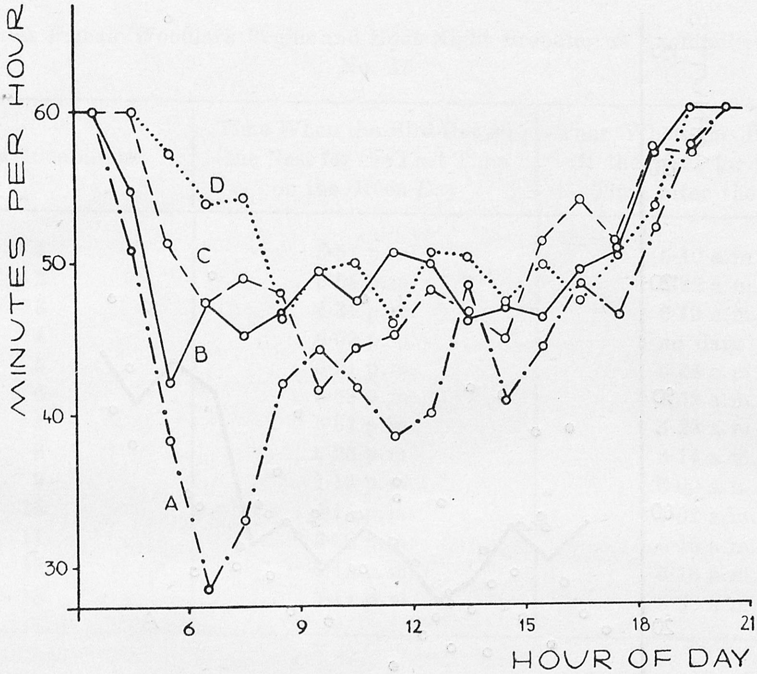


Fig. 20. Twenty-four hour pattern of intensity of incubation. The curves represent the mean values for the whole period of incubation in the case of females A and B and for the last six days of incubation in the case of females C and D

C. Diurnal Rhythm of Incubation. Figures 19, 20 and 21 show that the activity of sitting changes in the course of the day. The periods of sitting decrease from the moment of awakening till 10 or 11 a.m., when they reach their minimum length, to increase steadily till the female falls esleep in the evening. On the other hand, the length of breaks is independent of the time of day and maintained at approximately the same level from morning till night. The intensity of sitting, i.e., the number of minutes per hour during which the bird broods, changes like the diurnal activity only that it shows greater fluctuations in the morning (e.g., nests Nos. 15 and 5 — Fig. 20 A and B).

Observations made at night, before daybreak and after nightfall, confirm the opinion that females roost on the nest starting from the night preceding the laying of the fourth egg up to the 8th day of life of the nestlings. This is, therefore, the main period of incubation, covering about 9 night hours of uninterrupted warming. The length of these periods does not increase even towards the end of incubation and the hours at which the female gets off the nest depend on incidental factors, as will be seen from Table X.

Though remarkable, the differences between particular days cannot be explained either by the developmental stage of the embryo or by climatic changes. The female sat longest without let-up on the 9th day, from 1·15 p.m. to 5·47 a.m. on the next day, more than 15 hours.

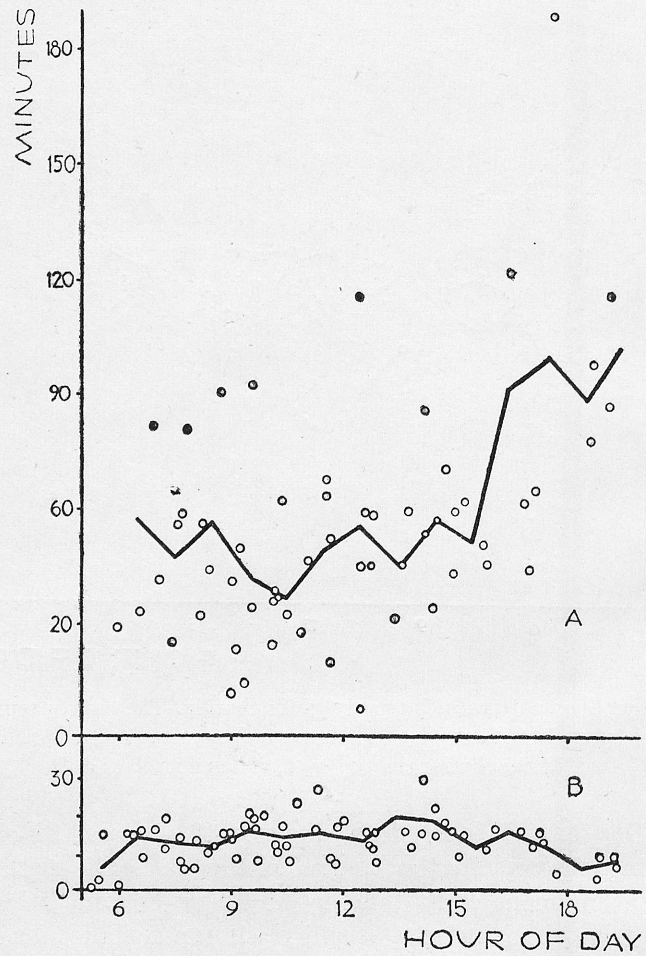


Fig. 21. Length of brooding (A) and length of breaks in brooding (B) in the daytime, on the basis of continuous observations of one nest from the 8th to 13th day of incubation (5130 minutes of observation). The solid line represents the mean from 6 days

The effect of weather conditions on the course of incubation is slight and temporary. Changes in temperature during one day or several consecutive days cause no visible changes in the activity rhythm. Cloudiness and wind also exercise only little influence. The most distinct influence is that exerted, though not before the second period of incubation, by heavy rainfalls, which lengthen the time of sitting and shorten the breaks, whereas during the long-lasting light rains females come off the nest even in the last phase of incubation. Never, however, do they leave the nest when it hails or snows. Female No. 2 was covered by a 3-centimetre layer of snow so that only its head jutted out above the surface.

A comparison of the results obtained by me for the Woodlarks with those

Table X

Hours at Which Female Woodlark Begins and Ends Night Brooding as Exemplified by Female No. 15

Day of Incubation	Time When the Bird Got on the Nest for the Last Time on the Given Day	Time When the Bird Came off the Nest for the First Time after the Night
1	5·51 p.m.	5·10 a.m.
2	5·55 p.m.	5·22 a.m.
3	4·34 p.m.	6·19 a.m.
4	6·09 p.m.	no data
5	6·21 p.m.	5·28 a.m.
6	5·58 p.m.	4·52 a.m.
7	6·01 p.m.	5·23 a.m.
8	6·23 p.m.	6·14 a.m.
9	1·15 p.m.	5·00 a.m.
10	4·11 p.m.	7·02 a.m.
11	5·59 p.m.	6·10 a.m.
12	5·13 p.m.	5·16 a.m.
13	7·11 p.m.	5·28 a.m.

of DELIUS (1963) with respect to the Skylark shows that the female Woodlark comes off the nest one-third of the number of times found for the Skylark, but stays away from it twice as long as the Skylark does. I have not checked whether DELIUS's findings are sound for the Skylarks nesting in the forest clearings of the study area. No doubt, these differences result from the different conditions of food acquisition. The larger share of animal food in the Woodlark's diet may also have an effect on the difference between the behaviour patterns of these species.

X. NESTLINGS

1. Hatching

As early as a few days before the hatching the female looks under its body and watches the eggs, but the day of hatching, at first, differs in nothing from the other days of incubation. The young hatch by themselves and it is only their movements that attract the mother's attention. Then the female pulls the egg-shell out carefully and removes it from the nest, but it does not do this, if the shell, though completely cracked, still encloses the wet young bird. Only in 6 cases (20%) out of the 30 observed the females interrupted incubation to remove a shell. In 80% of the cases (24) they noticed the shells on their return to the nest after a normal break in brooding. The impulse to remove the shells is, therefore, released chiefly by sight stimuli.

All my observations of Woodlarks show that females eat up the shells right on the nest or outside the nest, but do not carry them away to drop. The instinct of eating up is so strong at the time of hatching of the young that female No. 12, having eaten the shells, attempted to eat a dead leaf of birch that had been lying near the nest for several days. The egg-shells are removed chiefly by the female. Only in one case I saw the male carry out two shells one after another (Phot. 10). It was the male from nest No. 2, in which 3 young hatched in the evening, and the last, the fourth one, just before dawn on the next day. On this day both the male and female fed the young by turns from 4·45 a.m. After each feeding the female settled down on the nest to warm the young. As late as 6·52 a.m. the male, having fed the young, took an egg-shell out of the nest and carried it away to a distance of 20 m. At 7·02 the male returned to feed the young and again took a shell away, this time the last one, from the nest. At that time the female fed the young also, but it only cleared the nest of the excreta of the young. The egg-shells removed by the male had been lying in the nest for more than 12 hours unnoticed by the female. The removal of a young, chilled to death, by the male from nest No. 25 was another variant of this instinct. Out of the 30 egg-shells, 21 were eaten up by females on the nest, 7 were carried away by females to a distance of 10 m. and there eaten up, and 2 shells were dropped by the male about 20 m. from the nest. The directions in which the egg-shells were carried away were various.

The eating of shells proceeds as follows: the bird grasps the edge of a shell with its bill and crumbles it by small movements of the jaws. Sometimes a piece that has broken off falls on the ground; then the bird picks it up and swallows. It eats fairly quickly, taking on the average 45 seconds to consume one shell. If more than one young hatch at the same time, the female swallows the last shell with great effort, as if it lacked saliva. Even when disturbed, the female does not stop its action and does not move away before it has eaten up the last piece of the shell.

Although the birds remove the egg-shells, dead nestlings and even leaves from the nest, they leave the unfertilized and chilled eggs untouched throughout the period in which the young stay in the nest, as has been found in the cases observed.

The young hatch at different times of day. Three-quarters of them emerged from the shells from 4·00 a.m. to 2·00 p.m., which is probably due to the rhythm of incubation.

In one case I managed to note the exact time of hatching of a young. Fifty-seven minutes elapsed from the moment of puncturing of the shell to that of its being eaten up by the female. There are rather remarkable differences in the course of hatching between particular young. The first two chicks hatch within one hour, almost at the same time, and the last two often not before the next day. The maximum period of hatching, between the first young and the last, was 18 hours. In the nests with full clutches numbering up to 4 eggs, all the young usually hatch within 3—6 hours, whereas in a clutch of 5 or

6 eggs the last young, as a rule, hatches on the next day. This is probably connected with the commencement of incubation after the laying of the fourth egg.

2. Feeding of the Young

The male and female begin to feed the young in the first hours after the hatching of the first young. The female is always the first to start feeding. In nest No. 12 it tried to feed the young as early as 22 minutes after eating up the first half-shell, in nest No. 15 after 26 minutes, in nest No. 22 after 45 minutes, and in nest No. 25 after 60 minutes. However, the effective feeding of the first young took place as late as 4 hours 43 minutes after the female had eaten up the empty egg-shell. The sight of the feeding female stimulates the male to do the same. One of the males manifested a desire to feed the young at the beginning of the incubation period. It approached the incubating female with some food in its bill, but each time it did so, the female left the nest, as if under compulsion. Then the male looked into the nest, bent over it several times, but having found no young in it, moved away after a few seconds. After such visits of the male, which occurred rather rarely, at most once or twice a day, the female soon returned to the nest.

In nest No. 22 the male began to feed the young earliest, 66 minutes after the eating of the shell of the first egg by the female, i.e., 20 minutes after the twofold feeding of the young by it. In nest No. 12 the male fed the young for the first time after 87 minutes, when the female had already fed them 6 times. When the female fed the young in nest No. 25 for the first time, the male was still singing over the nest, which it approached with food as late as 7 hours 32 minutes after the female had eaten up the egg-shell and fed the young 5 times.

As will be seen from the foregoing examples, the female begins feeding within nearly one hour after the hatching of the first young, whereas the male takes to feeding later (in extreme cases 20 minutes and 6·5 hours after the female).

The first attempts of feeding are often failures. I observed a case in which the old bird ate the food itself, although it had tried to put it into the bills of the young more than 10 times. The young soon learn to take food from their parents and the time of feeding becomes shorter and shorter with their growth.

The first feeding goes like this: the male and female stand over the nest and utter calls in a low voice. The young can hear from the first moment and respond to their parents' calls by lifting up their heads (Phot. 11). Holding a small insect larva with the tip of its bill, the old bird tries to place it carefully in the gaping jaws of a young. If the young does not swallow the food at once, the trial is repeated. In order to induce the reflex of wider opening of the bill,

the female touches the open gullet of the young bird with its bill, nodding its head several times. In nest No. 12 the female put its bill into the gullet of the same young eight times during the first feeding, though it received most of the food at the fifth time.

One nestling usually receives the whole ration of food. If the ration is too large and the young begins to choke, it becomes divided into two parts; one is eaten by the young being fed and the other is swallowed by the feeding parent or given to another young.

The pattern of feeding presents several problems, which will be discussed in the next six subsections.

A. Frequency of Feeding of the Young. The frequency of feeding is influenced by three factors: the number of nestlings in the brood, the duration of their stay in the nest, and the intensity of feeding.

The amount of food which each of the young receives depends chiefly on their number. The nests covered by the present investigation contained 2—6

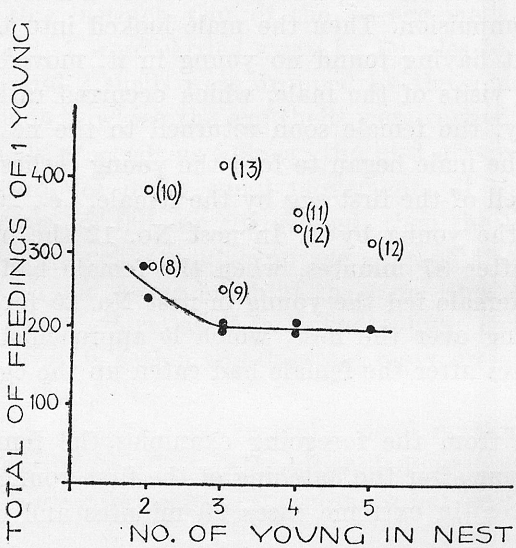


Fig. 22. Effect of the brood size on the total number of feedings of one nestling, on the basis of the data from 7 nests. The curve represents the mean number of feedings of one nestling up to the 8th day of feeding inclusive (black circlets). The bracketed figures by the white circlets indicate the last day of feeding of the young in the given nest.

nestlings each. The young of the least numerous broods got most food. This is clearly seen from the shape of the curve in Fig. 22. Each nestling was fed on the average 200 times (201, 198, 206, 196, and 199) during its stay in the nest.

The duration of the stay of the young in the nest varies fairly much, ranging from 10 to 13 days. Disturbances occurring unepectedly in the vicinity of the nest may scare the young and make them leave the nest 2 days earlier, i.e.,

on the 8th day after hatching. Under normal conditions the nestlings from small broods leave the nest earliest. A 10-day-old chick from a brood of 2 weighs on the average 22·675 g. at the time of its departure from the nest, whereas a similar specimen from a brood of 5 only 15·300 g. The weight of the latter, thus, forms hardly about two-thirds of that of the former.

The intensity of feeding of the young by particular pairs shows individual variation. It is undoubtedly conditioned by the availability of food, the distance of the feeding ground from the nest, and other factors. Pair No. 11 is an extreme example in this respect: it had 4 young in May and brought food to the nest as many as 244 times a day, in which it markedly exceeded the pairs with June broods of 5 young.

B. The Course of Feeding of the Young in the Nestling Stage. The changes in the frequency of feeding connected with the age of nestlings are illustrated in Figure 23, in which the curve represents the means from 8 nests varying in size of brood (2 broods of 2, 3 of 3, 2 of 4, and 1 of 5 nestlings). The changes in the frequency of feeding of particular nestlings during their stay in the nest are illustrated by the curve in Figure 24. An analysis of the curves in Figures 23 and 24 reveals 3 distinct periods of feeding:

The first period lasts from the hatching of the nestling to about the 4th day of its life. In general, the frequency of daily feedings increases slightly, though in many broods it even decreases on the second day as compared with that on the first day. This fact, however, does not mean a reduction in the

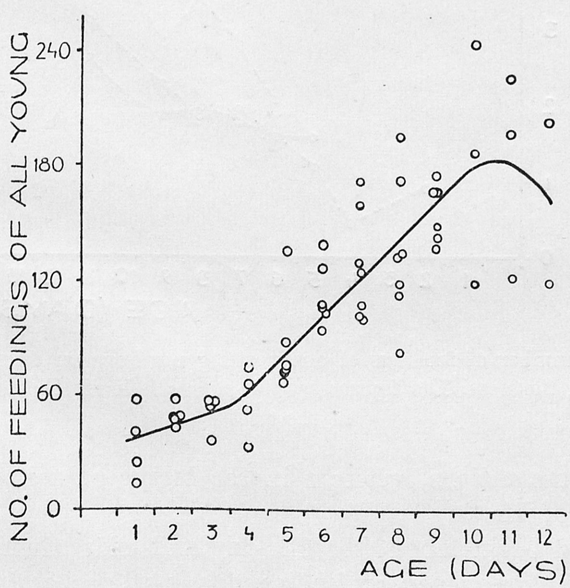


Fig. 23. Effect of the age of nestlings on the number of feedings per day, on the basis of the data from 8 nests. The smoothed curve illustrates the mean numbers of feedings in a brood of average size

mass of food, because the rations become larger and larger. In this period the female spends much time warming the young and yields to the male in feeding them (cf. Fig. 27).

The second period, more or less from the 4th to 10th day of life, exhibits a rapid increase in the intensity of feeding. It is marked by a strong and steady rise in the frequency of feeding. This period lasts shorter for small broods, ending between the 7th and 9th day, because individual nestlings of these

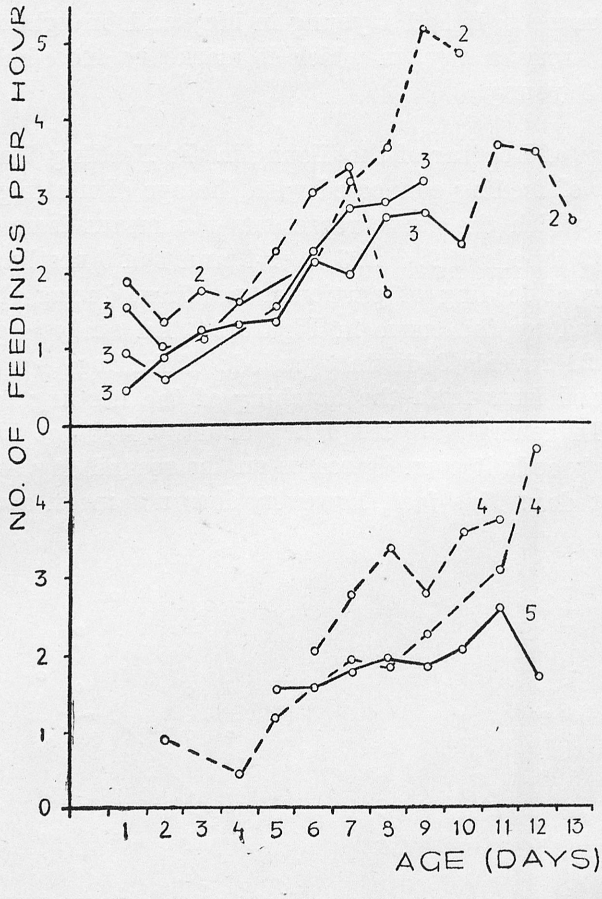


Fig. 24. The mean number of feedings of one nestling per hour on consecutive days of the stay of the young in the nest. The figures by the curves indicate the number of the young in the nest

broods receive more rations, whereas in the larger ones it extends even up to the 11th day of life.

The last period begins about the 9th day and ends when the young leave the nest. The daily frequency of feeding does not rise or is even somewhat reduced.

A comparison of the frequency of feeding in May with that in June and the observations published by Steinfatt (1939) show that the total daily

amount of food brought to the young converted into values per hour is lower in June than that obtained for May broods. This may be due to the lengthening of the daytime and, consequently, the time of feeding by 2 hours and a half, whereas the number of feedings per day remains similar, and to the higher ambient temperature resulting in a lower consumption of calories by the organism and a lower food requirement.

C. The First and Last Feedings during the Daytime. The pattern of feeding depends partly on the length of day. Since in the period of later broods the daytime is longer, the first feeding is shifted to earlier hours of the day and the last feeding to later hours.

In connection with the fact that at the end of June the periods of morning and evening twilight are markedly lengthened, in June the Woodlark begins feeding its young earlier before sunrise and feeds longer after sunset than it does in May.

In May the first feeding of the young before sunrise was a rare occurrence, and at the latest it took place 59 minutes after sunrise. On the other hand, in June feeding is commonly done before sunrise, and in the latest instance it was observed 45 minutes after sunrise.

The last feeding usually occurs after sunset, only exceptionally before it. The nestlings from the first half of June are fed on the average 20 minutes and those from the end of June 22 minutes longer after sunset than the young from the first half of May.

D. Diurnal Rhythm of Feeding. The feeding of young proceeds fairly uniformly in the daytime and is performed by both the male and female. The graphs illustrating the daily means (Fig. 25) show a slightly marked morning maximum between 5 and 10 a.m. for May broods and an evening maximum about 4 p.m. For June broods the morning maximum begins at 4 a.m. and the evening one is shifted to 7 p.m.

E. Intervals between Feedings of the Young. Direct observations of the nests and the determination of the shares of males and females in the feeding of the young made it possible to measure the intervals between particular feedings. These observations were made everyday during the stay of the nestlings in the nest. In the last four days of this period the parents brought food to the nest most frequently. The curves in Figure 26 illustrate the lengths of intervals between feedings in four nests varying in brood size, during this period. Most of the curves show that the modal interval falls in the group from 6 to 9 minutes. This is therefore the time the Woodlark nesting in pine plantations commonly takes to collect a ration of food for its young. In the period of most intense feeding in the case of nest No. 11 (4 young) and in the last two days as regards nest No. 18 (5 young) the modal interval was still lower, ranging between 3 and 6 minutes. The asymmetrical shape of the curves indicates that the measurements are influenced by several factors. This agrees

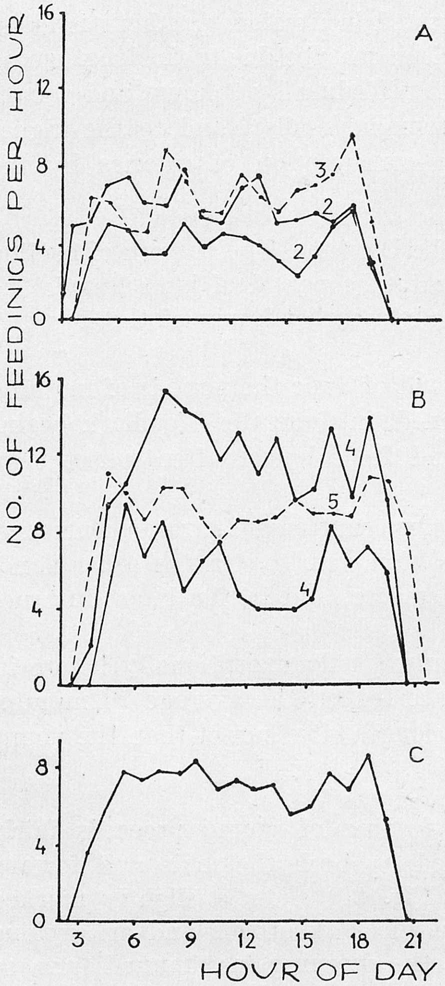


Fig. 25. The mean number of arrivals of old birds with food at the nest in particular hours of the day for the broods of 2 and 3 nestlings (A) and those of 4 and 5 nestlings (B). The figures by the curves indicate the number of nestlings in the nest. Curve C represents the mean value for all the May broods examined

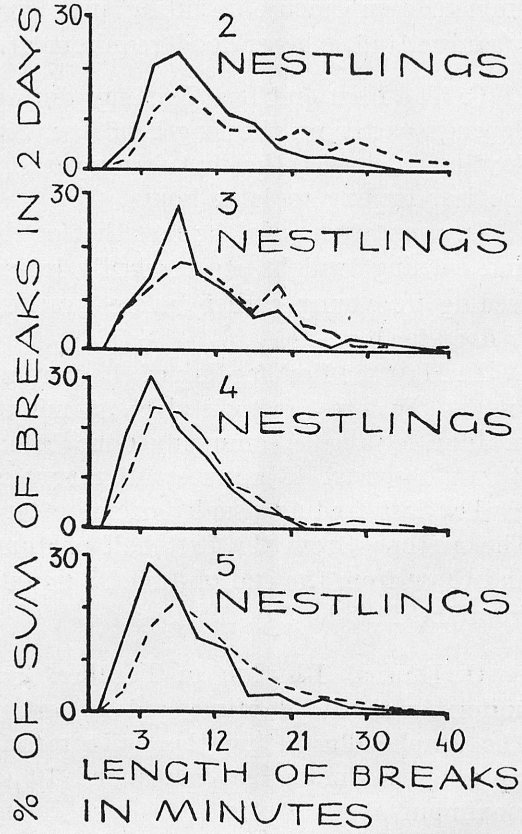


Fig. 26. The distribution of the lengths of intervals between feedings on days 8 and 9 (broken line) and 10 and 11 (solid line) of the nestlings' stay in the nest for broods of various sizes

with the data on the course of feeding obtained from observation, because in addition to the gathering of food, the old birds clean and trim their plumage, rest (chiefly males), respond to alarming phenomena in the surroundings, hide, etc. All these actions are done in the time in excess of the modal interval and corresponding to the descending slope of the curve in the graph. On the other hand, the initial portion of the curve represents the time given exclusively to the search of food.

A comparison of Figure 26 with the curve in Figure 18b shows that in the last phase of incubation the gaps in sitting on the eggs also average about 10 minutes, which confirms the now obtained length of time needed to collect food.

In order to find out how the intervals between feedings present themselves during the whole nestling stage, I carried out observations of 2 nests throughout this period. Males are not exclusively busy gathering food and feeding the young all the time and are less regular in this respect than females. The 7—9-minute-long breaks become more and more frequent from the 6th day onward, which proves that the parents often feed their 6-day young, without doing anything else, for several successive hours.

F. The Shares of Male and Female in Feeding. The young were fed by both the male and female in all the nests of the Woodlark observed. In the first hours after hatching the male brings food only at the sight of the feeding female. Soon, however, its share increases, because the female must, above all, warm the young in the initial period. Under unfavourable weather conditions, when the care for young includes their protection against rain in addition to warming, the male feeds the young much more intensely than the female. This predominating activity of the male lasts to the 4th day of life of the young, from which moment up to their departure from the nest both the birds occupy themselves in feeding their offspring almost uniformly, with a slight preponderance of the female's activity, as may be exemplified by the situation in nest No. 25 (Fig. 27).

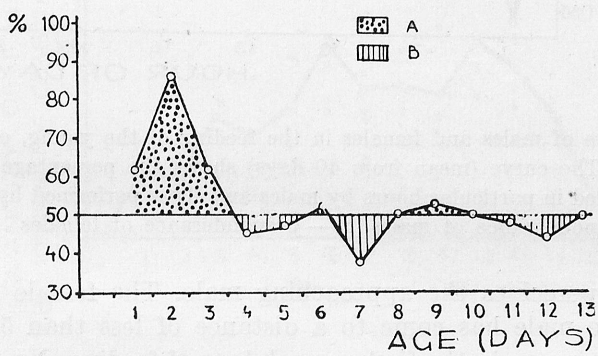


Fig. 27. Share of the male in the feeding of the young on consecutive days of their stay in the nest (data from 1 nest with 3 nestlings). A — preponderance of male, B — preponderance of female

To sum up, in particular nests the share of the male in feeding is smaller than that of the female by 0 to 5% except for nest No. 11, in which the preponderance of the male in this respect subsisted to the end of the period, exceeding the female's activity by 10%.

In the early hours of the day the male feeds more intensely than the female, which starving after brooding the young all through the night must first feed itself. In the further hours of the daytime the shares of both birds are nearly equal (Fig. 28).

In 80% of the cases the old birds return with food simultaneously. If the rate of feeding is not too great, the female is generally the first to approach the nest; the male feels less safe in the proximity of the young and for this reason observes the surroundings longer before coming close to the nest. When, after feeding the young, the female gets on the nest to brood them, it performs

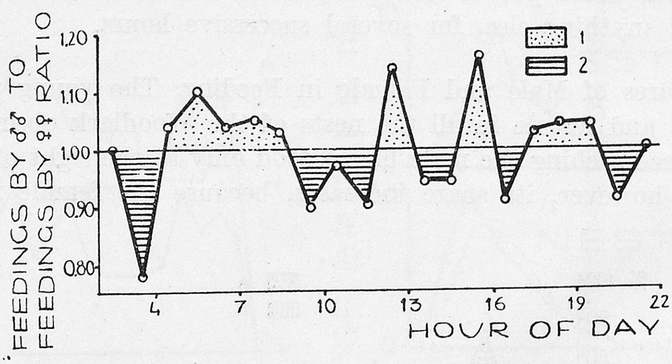


Fig. 28. Daily shares of males and females in the feeding of the young, on the basis of the data from 7 nests. The curve (mean from 40 days) shows the percentage relations between the feedings performed in particular hours by males and those performed by females. 1 — preponderance of males, 2 — preponderance of females

a half-turn and perceives the approaching male. The female leaves the nest hastily, when the male has come to a distance of less than 50 cm. Such behaviour is very common in the first several days of feeding. No doubt, it results from the fact that, though the birds gather food together and return to the nest together, the female does not realize the situation, and it is only the sight of the coming male that releases a proper response. In the later days of the feeding period the male more and more frequently comes up to the nest first. After feeding the young the birds fly away together. From the 7th day onward, in the case of big broods (more than 4 nestlings) both birds often feed the young together, standing side by side (Phot. 12). Krampitz (1952) failed to observe male Woodlarks bringing food for the young and confines their function only to the guarding of the female against enemies.

3. Attention to Nest Sanitation

Woodlarks remove egg-shells and faeces of the young from the nest in a similar manner, chiefly by swallowing them. Removal of addled eggs was not observed at all. I left such eggs purposely in three nests and they lay in

them untouched till the young birds had flown out. On the contrary, I never found a dead nestling left in the nest.

Once I succeeded in observing a male carrying a dead nestling away from the nest. It is, however, difficult to decide whether this behaviour is connected with instinct inducing the bird to remove the egg-shells or with the instinct to clear away the faeces. There seems to be a drive to clear everything away from the nest that is not an egg or a nestling begging for food.

The removal of faeces goes like this: having swallowed a ration of food, a young tumbles up its siblings and defecates on the rim of the nest. From the 5th day of life onward the young direct their heads towards the entrance, i.e., in the direction from which their parents come with food and, consequently, most excreta are discharged in the back part of the nest. The receiving and

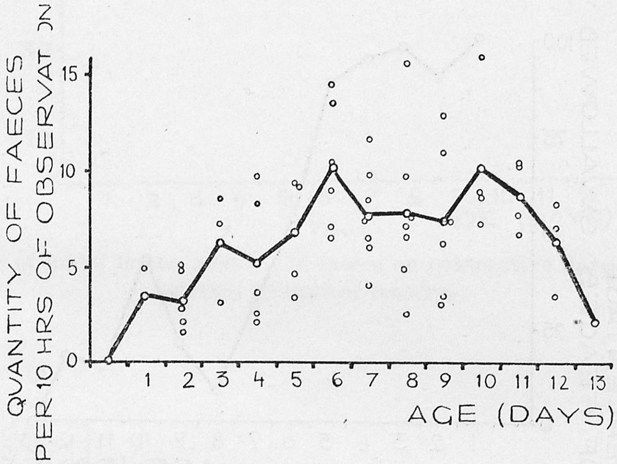


Fig. 29. Effect of the age of nestlings on the number of feacal sacs discharged (data from 8 nests)

swallowing of food, the turning of the hind part of the body towards the nest edge, and the evacuation of the bowels last 3—8 seconds (averaging 5 seconds). Then one of the old birds removes the faeces from the nest. When disturbed, the bird flies off from the nest without taking the faeces, which are left unremoved until the other bird does it on the occasion of the next feeding.

After feeding a nestling, a bird, especially the male, often shows hesitation whether to fly away or to wait for the nestling to defecate. I often observed a male waiting for a while after feeding the young; eventually it moved away to a distance of 30 cm. and returned again seeing the nestling have voided the faeces in the meantime.

Faeces of a young Woodlark, like those in other species of the *Oscines*, are white in colour, because they contain urea, and enclosed in a mucoid sac. Their absolute size grows with age of the young. The weights of faeces were 0·75 g. (9·6% of body weight) for 3-day nestlings, 0·77—0·80 g. (4·6—6·1%

of body weight) for 6-day nestlings, and 0·90—1·00 g. (4·5—5·4% of body weight) for 7-day-olds. The percentage rise in the weight of faeces is, therefore, smaller than that in body weight. The number of feacal sacs discharged by a young in a unit of time increases in the first 10 days of life and next drops evidently (Fig. 29).

The consistence of faeces, originally semi-liquid, becomes denser with age of the young. In a few of the cases observed, the faeces of the young leaving the nest (12 days of age) already looked like those of old birds. In addition, in the faeces of older nestlings (from the 10th day onwards) one can see pink excretion of the appendix. Watery faeces observed in several nests were probably due to diarrhea caused by protozoans.

An old bird takes a faecal sac in the tip of its bill and either, having thrown it up, swallows it on the spot or carries it away to a distance which varies

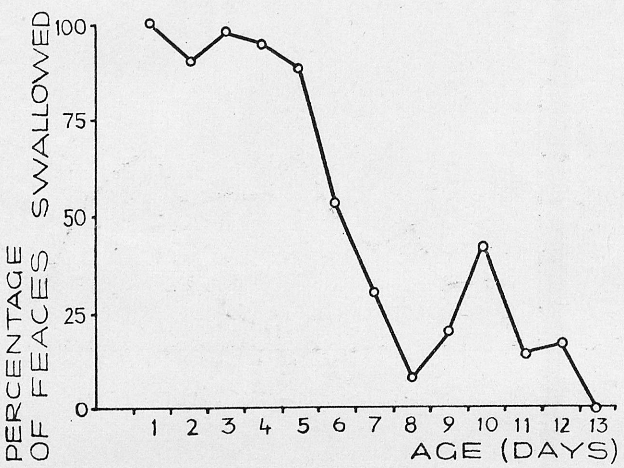


Fig. 30. Effect of the age of nestlings on the removal of faeces by swallowing as exemplified by 1 nest with 3 nestlings

even for the same nest. Most frequently, the birds fly away with the faeces and drop them after alighting or still on the wing. Having done this, they immediately clean their bills against the ground. According to my observations, the shortest distance to which a bird removed the facces of the young from the nest was 10 m.

The swallowing of faeces depends on their size and amount per time unit. During the first days of nestling life the old birds swallow all the faeces of the young. As the amount of faeces increases, the number of faecal sacs swallowed drops. In nests with big clutches the quantity of faeces swallowed falls more rapidly. From the 7th day of nestling life 70% of the faeces cleared away by the female and 90% of those removed by the male are carried away and only the rest of them swallowed (Fig. 30). Broods of 2 nestlings are an exception in which the Woodlarks eat up most of the faeces (female — 75%,

male — 59%) up to the end of the stay of the young in the nest. In nearly all nests the birds swallow a certain, however small, amount of the faeces even on the last day.

The share of males in the removal of faeces somewhat exceeds that of females (Phot. 15). Males make it look as if they simply watched for the op-

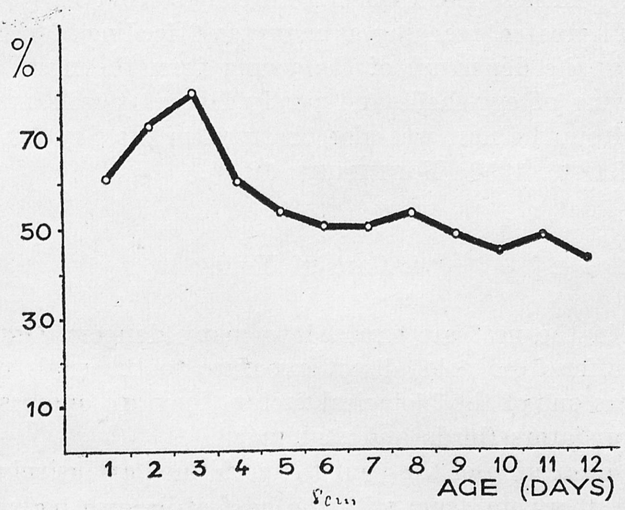


Fig. 31. The share of males in the removal of faeces on consecutive days of nestling life in relation to that of females.

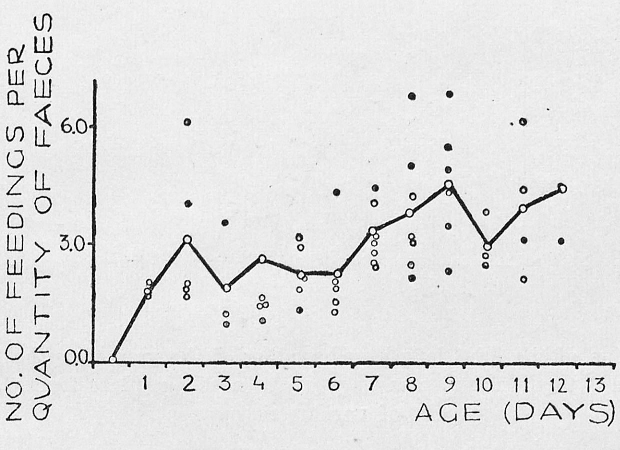


Fig. 32. Effect of the frequency of feedings on the number of defecations (data from 8 nests)

portunity to remove faeces of the young. The females often got on the nest without clearing away the faeces, which never occurred to a male. As the males are more skittish in the proximity of the nest, their care may be explained only by a stronger instinct to remove (Fig. 31). As late as the 7th day, when the period of brooding the young comes to an end, the female gets ahead of

its mate in this respect. The situation resembles the share of both parents in the feeding of the young, but it is more conspicuous.

In order to examine the correlation between the frequency of feeding and the number of faecal sacs voided by the young, the ratios of these values were calculated for the time of their stay in the nest (Fig. 32). This ratio rises with nestling age, e.g., in nest No. 25 nearly threefold, from 1·28 to 3·66. In other nests it was still greater, reaching as many as 6 feedings for 1 defecation immediately before the departure of the young from the nest.

The swallowing of egg-shells and partly faeces as well as the removal of dead nestlings from the nest was also observed in the Skylark (Delius, 1963; Hesse, 1917; Lewis, 1959; Mountfort, 1940).

4. Care of Young

The young in the nest are exposed to many dangers. Out of the abiotic factors, they suffer from cold, direct exposure to the sun's rays, and precipitation, whereas out of the biological factors they are oppressed by parasites and different predators (birds and mammals).

The task of protection of the young is performed exclusively by the female. When it is cold, it warms them with the heat of its own body, and it shelters

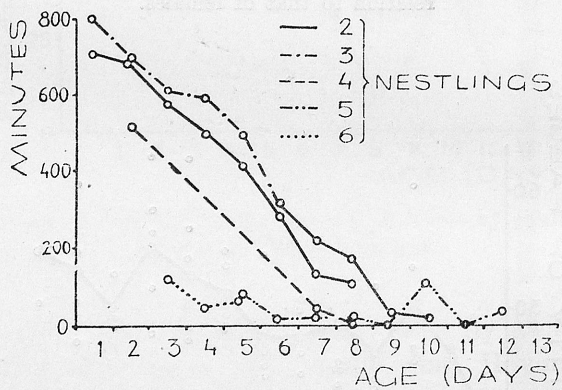


Fig. 33. The relation of the joint length of brooding of the young by the female in daylight (from dawn till dark) to the number and age of the nestlings (data from 5 nests with broods of various sizes)

them under its wings during the rainy weather and from the scorching rays of the sun.

The brooding of the young is, in a sense, the prolongation of incubation. It differs from incubation in the fact that the female interrupts it more frequently. The duration of brooding the young in the daytime depends on the intensity of feeding, which increases with age of the young. It also depends on the number of the young in the nest. In nests with 4 or 5 nestlings the

female gives up brooding almost completely on the 5th day of nestling life. In 3-young broods it does this on the 6th day, and broods of 2 nestlings are warmed up to the 8th day. The results of observations concerning the protection of the young are presented for five nests in Figure 33.

On the first day, immediately after hatching, the brooding of the young practically resembles egg incubation. However, as the nestlings grow, the female stands higher and higher over the nest. Older nestlings often put their heads out from under its feathers. Brooding the young differs from incubation

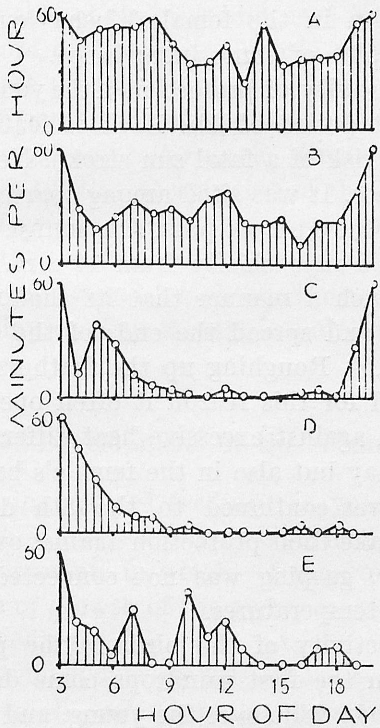


Fig. 34. The brooding of the young by the female on the second (A), fifth (B), seventh (C) and eighth (D) days of life shown by the example of a nest with 2 nestlings. Graph D shows that the female roosts outside the nest after the eighth day. Graph E illustrates the protection of 2 nestlings in another nest against the sun's rays on the 8th day of their life

in that the female lifts its body up one or two centimetres every now and then for a young to change its position. The female behaves in a particularly characteristic manner when it is asleep. It rises rhythmically at intervals, moves to the back, and looks at its young.

At the beginning the female broods the young day and night, next it confines itself to the night and to the morning and evening hours in the daytime, in the end only to the night (Fig. 34). The female ceases brooding its young on the average on the 9th day of nestling life and from this time onward it roosts outside the nest. The shortest period of night brooding observed by

me was 8 days, its longest duration being 11 days, after which the female slept crouched in the grass about 2 m. from the nest. The shortening of the brooding time before the completion of fledging of the young would indicate that, e.g., on the 5th day, in the case of larger broods they are big enough to fill up the nest and thus able to secure themselves against the loss of heat. On the other hand, 3-day-old nestlings, if left uncared-for in cold mornings, may be chilled to death. With a larger number of nestlings in the nest the brooding time is reduced not only because the old birds must devote more time to feeding them but also on account of the more favourable thermal conditions in such nests. Individual variation in the females' behaviour, while brooding their young at night, is here also of some importance.

There may occur a necessity of protection of the young against the excessive sun radiation in the first period of life. Lack of feathers makes young birds particularly liable to the risk of a fatal sun stroke. Nest No. 12 was examined more closely in this respect. It was sited among sparse grasses of a 4-year pine plantation, 30 cm. from the nearest pine. On sunny days the female shaded the young from the sun's rays chiefly from 10 a.m. to 2 p.m. Standing on the rim of the nest in such a manner that its shadow fell on the young, it roughed up the feathers and spread the ends of the wings so as to augment the shaded area (Phot. 16). Roughing up the feathers made the female liable to overheat its body and for this reason it often opened its bill and gaspad. Therefore, the protection against excessive heat differs from that against cold not only in time of the day but also in the female's behaviour. The protection from excessive sunlight was continued to the 8th day. On the 6th day the young themselves undertake their protection against overheating, gasping with their bills open. However, gasping was not connected directly with sunlight but with high ambient temperatures.

Another important activity of the birds is the protection of the young from precipitation. When the first raindrops come down, the female returns to the nest, spreads its body wide over the young, and remains in this position, with its feathers roughed up, till the rain has stopped. It generally gets off the nest 2 or 3 minutes after the rain and, having shaken off the raindrops from its feathers, runs in search of food. One nest was watched during a hailstorm. The male took shelter in the nearby young growth, but the female sheltered the brood, shrinking under the blows of hailstones, up to 8 mm. in diameter. The protection from precipitation is particularly conspicuous in the first period after hatching. In nest No. 22 a spell of bad weather limited other activities of the female to the extent that the feeding of the nestlings was performed almost exclusively by the male for the first three days. The female did nothing but brooded the young except the rare moments when it came off the nest to refresh itself.

The protection from unfavourable weather conditions ends when the young leave the nest. If this falls in the period of cold and rainy weather, all the young may perish, as exemplified by the brood from nest No. 26. Five young

left this nest at 7 a.m. Owing to the rain and constantly wet grass, one young ceased calling for food immediately after leaving the nest, other two before 10 a.m., and the last one about 11 a.m. The old birds kept calling, holding food in the bill, but could not find the young. Their own feathers were wet through and they were in agony themselves.

Woodlarks are infested by a great many parasites. Scabs may often be seen on the bellies of the young in consequence of the bites of small ticks *Dermanyssus avium* brought into the nest in the plumage of the incubating female. As early as the first day after hatching the old birds begin to pick out parasites from the inside of the nest and next from the heads of the nestlings, which they do more and more frequently in the later days.

The young in the nest are also protected against other species of birds. When, for instance, a fledgling running out of the nest had been attacked by a Red-backed Shrike *Lanius collurio*, the female rushed at the aggressor and the fight did not stop till the intervention of the observer. The appearance of a Starling *Sturnus vulgaris* in the neighbourhood of the nest also stimulated the male to defence. On the contrary, the approach of a Cuckoo *Cuculus canorus* made the female cling to the ground just beside the nest. In one case it remained in this position for 28 minutes. This is a typical attitude of Woodlarks towards birds of prey (Naumann, 1900).

5. Development of the Young

Owing to the increasing rate of feeding the young grow fast and during their stay in the nest they increase about eightfold in weight (Fig. 35). The absolute and relative increments in weight of the young are shown in Figures 36 and 38. Three periods of growth of the young may be distinguished similarly to those in regard to feeding:

1. The period of postembryonic growth covers 2—3 days and is associated with the resorption of the yolk-sac and marked by a small frequency of feedings. Because of very slight differences some authors unite it with the next period (Haartman, 1954).

2. The period of rapid growth is, in Dortmann's opinion (after Haartman, 1954), constant for and typical of a given systematic group. In the Woodlark population under study it lasted up to the 9th—11th day, as may be seen from Figure 35. The weights of nestlings on particular days, illustrated in the form of a graph, present an almost straight line which ascends steadily. The fluctuations in the duration of the rapid growth period are governed by the brood size. The period is shorter in smaller broods.

3. Period of slow growth. Towards the end of the stay of the young in the nest (approximately on the 10th day) the increase in weight becomes slower. Unfortunately, the young repeatedly disturbed by weighing leave their nests earlier and thus make it impossible to measure the length of the period exactly. At any rate, it ends after the young have left the nest.

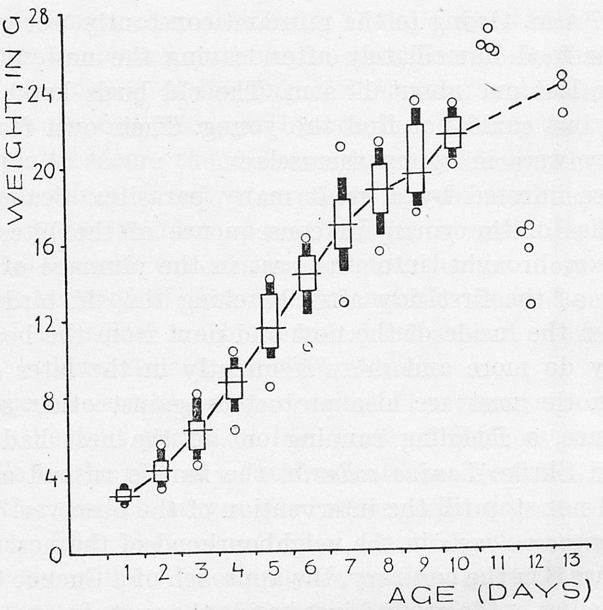


Fig. 35. The weight of the young on successive days of their life, on the basis of the measurements taken on 16 nestlings. The circles represent the extreme values, the black blocks 80% of the intermediate measurements, the white blocks 50% of the intermediate measurements and the horizontal lines the medians

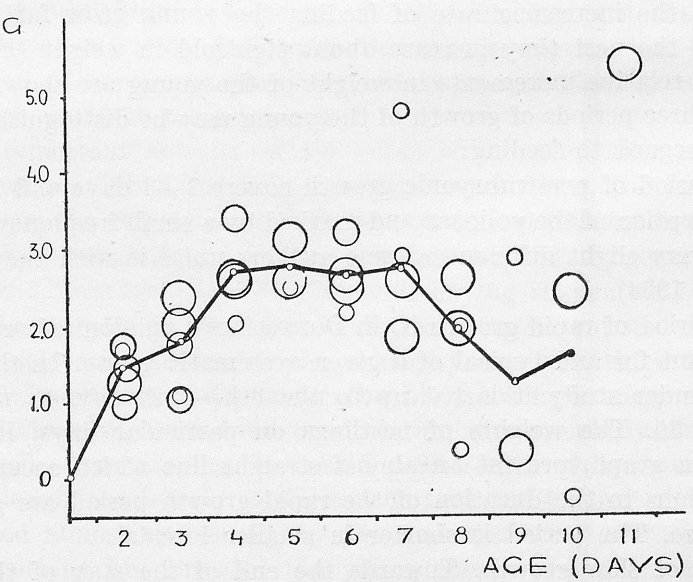


Fig. 36. Daily increments in weight of 16 nestlings. The diameters of the circles are proportional to the number of the young in the nest (2, 3, 4). The place of the circles indicates the mean increment for all the nestlings in the given nest. The curve represents the mean increment for all the nestlings examined

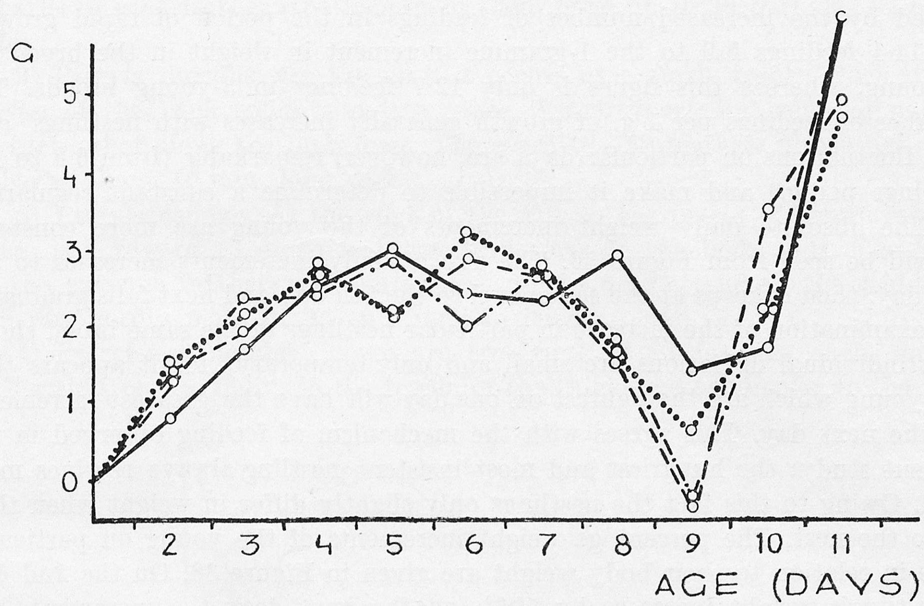


Fig. 37. Changes in the daily increments in weight of particular nestlings from one nest

Table XI

Mean Daily Increments in Weight of the Young from 5 Selected Nests in the Period of Rapid Growth

Nest No.	No. of Young in the Nest	Mean Daily Increment in Weight of One Young, in g.	Remarks
5	2	2·2790	May broods
12	3	2·9939	
10	4	2·5412	
11	4	2·5010	
18	5	1·1800	June brood

The daily increments in weight of the specimens from different nests in the period of rapid growth are shown in Table XI, which confirms the general regularity, found by Haartman (1954) and consisting in the fact that the young of medium-sized broods have the highest increments in weight. The smaller increments observed in bigger broods result from malnutrition, whereas those in broods of 2 young may be explained by a reduced persistence in calling for food and increased heat losses. According to Haartman (o. c.), in the Pied Flycatcher this phenomenon does not occur unless there is only one young in the nest. In the Woodlark, however, the heat losses caused by the open form of nests and their placement on the ground must be higher, if the presence of two nestlings in a brood results in their smaller weight. Their higher heat losses and, consequently, greater calorific requirements are illus-

trated by the increased number of feedings in the period of rapid growth, for 14·4 feedings fall to the 1-gramme increment in weight in the broods of 2 young, whereas this figure is only 12·7 feedings in 3-young broods. The number of feedings per 1 g. of growth generally increases with nestlings' age. The fluctuations on particular days are, however, remarkable (from 6·8 to 156 feedings per g.) and make it impossible to determine a constant regularity.

The absolute daily weight increments of the young are more constant, as will be seen from Figure 36. The size of daily increments increases to the 4th day, then it keeps at the same level to the 7th day and next falls gradually. An examination of the increase in particular nestlings of the same brood shows that individual deviations are small and only temporary, for it appears that the young which are the lightest on one day will have the greatest increments on the next day. This agrees with the mechanism of feeding observed in the present study: the hungriest and most insistent nestling always receives most food. Owing to this fact the nestlings only slightly differ in weight when they leave the nest. The percentage weight increments of the young on particular days in relation to their body weight are given in Figure 38. On the 2nd day a nestling's weight increases by 50%, on the next days the increments are smaller and smaller, falling to 10% on the 8th day.

The morphological and ethological changes of the young are far more striking than those in body weight. It is worth while to discuss them more fully, since there are no detailed descriptions of develpmental changes of young Woodlarks in literature.

First day

Immediately after hatching a nestling lies curled up and wet in the broken fragments of the egg-shell. At that time it weighs 2·00—3·07 g. It gets dry in an hour and, being intensely fed, puts on weight rapidly.

The trunk and head are yellowish, the crown of the head is bluish-grey with white dots marking the places of future feathers. The eyes are dark grey hemispheres and the bill is pale brown with an egg-tooth at the tip. The legs are yellow, paler than the body, the claws similar in colour to the legs except for the hind claw, which is pale brown. The tips of claws are curved at an angle of 30° to the toes. The pterylae on the back are brownish, the breast is yellowish with a strongly projecting sternum. The belly is yellowish flesh-coloured, with dark-coloured intestines visible through the skin in its middle part and the yolk-sac protrudes nearer the anus. The whole body is covered with whitish down, tinged light yellow-brown and grouped in the pterylae.

1) Pteryla capitis. On the crown of the head it includes only the frontal and parietal regions and consists of 8 down feathers disposed in 2 rows. Each feather has 10 barbs, 6—7 mm. long, with barbules, which become gradually shorter towards the tip of the feather. On the occiput a row transverse in relation to the body axis is separated from the head pteryla by a small bare area. This row consists of 8 feathers with barbs 8—15 mm. long. There are

9 barbs in each feather (the longest of them have up to 30 barbules on either side).

2) Pteryla dorsalis. On the neck it occurs as a single tract, which in the region of the back splits into two zones, 3 mm. apart and running parallel to each other along the body axis. There are 18—22 feathers altogether, with 9 barbs about 10 mm. long each.

3) Pteryla caudae. At the edge of the tail, in the places of future retrices, there is a row of 13 down feathers, transverse to the body axis. The barbs of the extreme feathers are the longest, up to 6 mm., and in the middle of the row hardly marked, up to 1 mm. in length.

4) Pterylae femorales. There are two rows of 13 feathers each, one on either side, on the flanks in the region of the thighs, perpendicular to the body

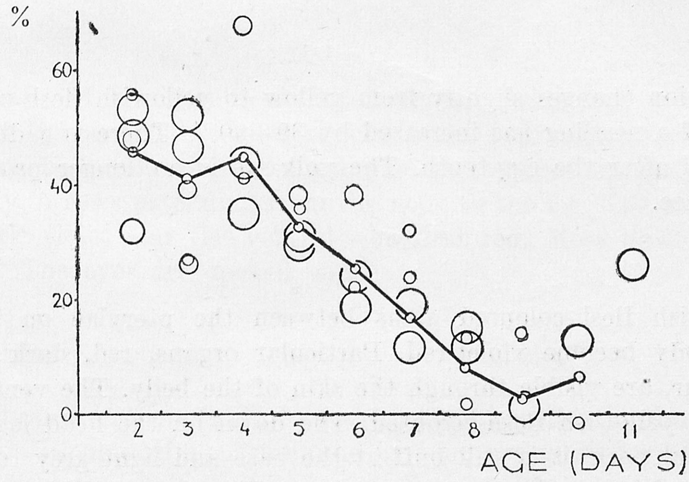


Fig. 38. A relative increase in weight of 16 nestlings within 24 hours during their stay in the nest expressed in percentages of the weight of the given nestling on the previous day. For diameters and places of the circles see the explanation of Fig. 36

axis, and in the extension of the tail feathers (3). Each feather of these rows has 9 barbs, 7 mm. long.

5) Pterylae humerales. A row of feathers, parallel to the body axis, is situated on either scapula. It is composed of 6 down feathers, 6—13 mm. long.

6) Pterylae alares — two tracts with shortest feathers: 1 row of 7 down feathers on the forearm, growing on the posterior margin of the wing, in the places of future remiges (length of barbs — 1—2 mm.), and hardly perceptible down feathers on the palm.

A one-day nestling has its down best developed in the occipital region of the pteryla capitis and in the pteryla humeralis. The down in the pteryla dorsalis, pterylae femorales, and the frontal and parietal regions of the pteryla capitis is shorter, being shortest on the tail (pteryla caudae) and hardly visibel

on the wings (pterylae alares). There is no down on the ventral side of the body at all.

The total number of the down feathers all over the body is 133 in 13 separate tracts. This number of feathers is sufficiently large to cover the nestling lying in the nest.

The inside of the mouth is sulphur-yellow with four black spots. The flange of the mouth is yellowish-white.

At first the young sit in the nest without keeping any definite direction, but after a few feedings they group in the middle of the nest. They hear from hatching and respond particularly strongly to a low whistle. They do not see, neither do they utter any voices. When taken out of the nest they are able to move on the substratum by putting the head under the body and thus pulling it forward.

Second day

The coloration changes slightly from yellow to yellowish flesh-colour. The body weight of a nestling has increased by 30—60%. There is a distinct sign left on the bill after the egg-tooth. The yolk-sac is no longer prominent on the belly surface.

Third day

The yellowish flesh-coloured areas between the pterylae on the dorsal side of the body become violet-red. Particular organs, red, dark grey, and yellow in colour, are visible through the skin of the belly. The ventral aspect of the body is yellowish flesh-coloured. The down on the head is grey now, whereas in other parts it is still buff at the base and light grey towards the end. The claw of the hallux is 2·5 mm. long. The young still respond to all sorts of voices, most vividly to low whistles. They also open their bills in response to shakes of the nest and the striking of the ground with a hand.

Fourth day

The upper side of the body becomes still darker in colour. The skin in the region of the dorsal and head pterylae is dark grey and the remaining part of the back has a reddish-olive tinge. The ventral side of the body is still pink-yellow flesh-coloured. The first yellow flesh-coloured shafts of remiges have grown out on the wings (2—3 mm. long) and those of coverts on the nape (1—2 mm.) as well as on the ventral side of the body in 3 paired abdominal rows and 8 breast rows. The liver can still be seen, red in colour, through the skin and the intestines steel grey. The first down feathers of the tail are being shed. The hind claw is not horny and it is 2·5—3·0 mm. long. The length of the bill is 6 mm. (3 mm. to the nostrils). The young scramble helping themselves with the wings; they can rise on the legs and, when laid down on the back, return to the normal position.

Fifth day

All the areas of the dorsal pterylae are dark grey. The shafts of the primary and secondary remiges are 4 mm. long and violet-black at the base and light brown at the end, whereas those of coverts in the pterylae of the head and back are 3 mm. in length. The eye slits are slightly opened (up to 2·5 mm.) and the young can already see. As a result, they do not open their bills, when an observer imitates the call notes of their parents.

Sixth day

The shafts of remiges are up to 7 mm. long and have a dark basal part. The dorsal apteria are bluish and the ventral ones pink flesh-coloured.

Seventh day

The shafts of remiges, 8—9 mm. long, are dark grey with light brown 3-milimetre tips and those of dorsal coverts, 5—6 mm. in length, are the same colours (tips 1—2 mm. long). The pterylae gastrae run obliquely on the flanks of the body, 5 rows extending from the neck to the leg. The back of the body is still dark violet and the ventral side flesh-red. Most down feathers have been shed. The eyes are opened wide.

Eighth day

The vanes of feathers begin to develop; in 15-millimetre remiges they have unfolded for a length of 4—5 mm. and in 7-mm. rectrices for half their length. Emerging from the shafts, the vanes of all the feathers are a subdued brown-black colour, edged pale yellowish, 3 mm. in width. The shortest shafts are those on the head (6 mm.). The hind claw is 5—6 mm. long. A nestling returns to the nest by itself from a distance of 1 m., spreading the wings to keep its balance.

Ninth day

The back is completely fledged. The coverts are dull brown-black with flaxen edges. The vanes of remiges develop for a length of 7 mm. and those of coverts are still longer. The eye-stripe is slightly marked, although the feathers are here still vaneless whitish shafts. The dorsal apteria are violet-grey and the ventral ones bluish-red. The feathers in the pteryla gastrae (Phot. 17) are cream-whitish and there are some dozen tufts of down on the head and rump. The claw of the hind toe is 6—7 mm. long. An excited nestling raises its crest and in danger it runs away from the nest. Among grasses it moves by hops. It utters call notes *tseep, tseeseep,* signalling where it is at the moment.

Tenth day

The eye-stripe is distinct and cream-white in colour. The remiges are 15—26 mm. long, and their vanes spread for a length of 8—9 mm. The vanes of rectrices are 8·5 mm. long, whereas the length of the claw of the hind toe is 6·2 mm. and that of the bill 5·9 mm. The flange of the mouth is on the wane.

When looking for their parents, the young call *whee tsitsits* and they also use these notes later, even out of the nest. During feedings they utter a series *tsee, tsee, tsee, tsee,* which somewhat resembles the notes of young Starlings or Woodpeckers.

Eleventh day

The primaries average 25 mm. in length. The ventral apteria are almost entirely covered by the feathers of the neighbouring tracts.

Before feeding, the young run out to meet their parents. When disturbed, they rush out of the nest and, while out of the nest, they move by jerks and hops. They can stand in a normal manner on their legs, not on the heels as before, for a fairly long time. In excitement they raise their crests. They know the close vicinity of the nests excellently and, when leaving the nest, look about in an uneasy way, like their mothers.

Twelfth day

The feathers are completely developed; black sheaths are still visible on the lore only. The eyelashes are yellow. The feathers in the dorsal pteryla have a grey-blue base, the rest of the vane being almost black with a white-yellow edge. The feathers in the head pteryla are similar in colour and those of the pteryla gastrae cover the whole underparts of the body. The belly is snow-white, the throat cream-white and the breast pale rusty with black spots, which, unlike those in adults, are roundish (Taczanowski, 1882). The yellow-white eye-stripes join at the back of the head. The edges of feathers are not uniform in colour: they are white-yellow in the middle, by the shaft, becoming more rusty towards the sides. There are a few tufts of down on the body. The bill is 7·5 mm. long, pale grey at the base and growing darker towards the tip. At the tip of the upper mandible there is still a white spot left after the egg-tooth. The flanges are still 8 mm. long and marked by their cream-yellow colour. The legs are pinkish, with the cream ankle bone visible through the skin from behind. The length of the tarsus varies between 18 and 23 mm. The claw of the hind toe is 7 mm. long, with a dark streak on the bottom side.

When out of the nest, the young move running. They can fly a distance of 50 cm. at a height of 30 cm. In addition to the call notes *whee tsitsit,* they occasionally utter a coarse and lower note *geet,* which afterwards changes

into *dluit,* the call note of adult birds. When caught by the wings or in another manner, a nestling utters a note of anxiety, a low and shrill *"geerreet",* resembling the call of anger of the male.

Thirteenth day

There is no down. The pale cream flanges of the mouth are still slightly marked. The black spots on the tongue are still present, but the grey ones inside the bill are vanishing. The inside of the mouth is yellow. Lengths: tail — 22 mm., bill — 8 mm., claw of hind toe — 7·5 mm. The nestlings from medium-sized broods may still stay in the nest, but usually they leave it at this time. They can fly a distance of 10—11 m.

Not only the external appearance but also the behaviour of the young changes with their age. For the first two days they lie at random on the floor of the nest, on the 3rd day they all turn towards the middle of the nest, and from the 5th day onward, keep their heads directed towards the parents coming with food. During the next days the young respond to their approach earlier and earlier. The direction of the imbricately arranged heads of the young will not change up to the end. From the 9th day onward, the most energetic nestlings come off the nest to meet their parents.

In the first days of life the young lift their heads quietly and open their bills noiselessly. As their sight develops, they perform swinging movements of their heads in a definite direction. At the end of the 6th day they utter their first low begging notes *tee, tee, tee.* At first the notes are single and low, hardly audible at a distance of 1 m.; with time they change into an insistent chorus. They grow louder and louder and reach a maximum at the moment when food is placed in the bill of one of the nestlings. Next the noise subsides slowly to stop after the departure of the old bird. If, however, the male and female feed the young immediately one after another and one of the parents remains at the nest waiting for a nestling to void faeces, the young give up calling in spite of its presence.

Sitting in a normal manner in the nest the nestlings fill it completely. From the 9th day onward, they respond to the arrival of the parents by lifting their heads. While waiting for their parents, they lift up the heads to a height of 3 cm. and at the moment of feeding as high as 5 cm. After the departure of the parents, the young still remain on the alert, with their necks craned, for a few seconds.

6. Time of Departure from the Nest

Young Woodlarks, like the young of other species of the *Alaudidae,* leave the nest before they have attained the full capability of flying. They are prompted to do this by the fact of nesting on the ground.

The last days of feeding are a kind of preparatory period for the young birds leaving the nest. They hear and see the approaching parents and to accelerate the feeding hop on to the rim of the nest. At first such responses occur at irregular intervals but they become more frequent with time. The hungriest nestlings usually rush out of the nest. Hence, in large underfed broods this process assumes a more conspicuous form than in small broods. The brood of 5 young from nest No. 18 were fed insufficiently and, consequently, this period of the nestlings running out to meet their parents lasted here longest — 3 days, whereas in nest No. 17 with 2 nestlings this period was confined to the last day.

A nestling may sometimes be seen to run treading on the heads of the siblings, especially when it has found its error in the direction taken up to meet the coming parents. However, the run mostly ended in feeding and, having swallowed the bit, the nestling returned to the nest and squeezed in between the other siblings. If a nestling ran too far from the nest, it might be overlooked by the feeding bird. On the last day, just before leaving the nest, the nestling moves away up to 40, and sometimes, 80 cm.

Finally, the most active nestling does not return to the nest after feeding, but follows its parents. When leaving the nest, the young cannot see the departing parents, but walks in the direction from which they usually approach with food. It remembers the way in the close neighbourhood, within a radius of 1·5 m., farther from the nest it gets lost amidst the high grass. Soon the remaining nestlings join it, too. Often, however, the last nestling, probably the weakest one, stays in the nest longer and is fed by the parents still for some time.

The young normally leave the nest between the 10th and 13th day of life. If disturbed, they may depart earlier, even on the 8th day. Such an earlier departure from the nest may be caused by a sudden threat of danger, e.g., the appearance of a man. An assault of a Red-backed Shrike or Jay at 10-day-old fledglings, ending in the capturing of one of them, makes the other siblings run away in various directions.

Out of the nest the young birds hide by squeezing in under the tufts of grass, sedge or biliberry shrubs, where they are difficult to find. They betray their presence by notes which they deliver every now and then, unless they feel that they are being observed or hear the warning notes of their parents. If they keep quiet, it is difficult even for their parents to find them. Young Woodlarks scatter rapidly over a small area, and although I have not observed them coming close to each other, they stay in the same wood plantation. In spite of their being scattered they still look for their feeding mother. The notes uttered by a fledgling while being fed still more provoke the others to search for their parents. Feeding particular fledglings in different places, the old birds prevent their concentration. Hence, the whole family is in constant motion.

XI. FORMATION OF FLOCKS

It has been known for a long time that after the young have been led out of the nest, Woodlarks keep in small family flocks till the autumnal departure (NAUMANN, 1900; WITHERBY et al., 1948; SCHUMANN, 1959; KOFFÁN, 1960). In autumn these flocks join into larger ones and fly away together.

If the old birds produce a second brood, the juveniles from the first brood (e.g., nest No. 18) stay nearby, but always out of the area in which the former forage. Thus, flocks of 2—4 young birds, capable of flying and uncared for by old birds, encountered late in the spring indicate that the parents have started to rear the second brood (3 juveniles stayed in the vicinity of pair No. 18 in the same plantation).

Some time later, the family flocks usually leave the nesting areas for more opulent feeding grounds, which at first little differ from the previous ones, and thus the birds feed in very young plantations, unwooded felling areas and those overgrown by brushwood amidst a forest. In the moulting season they most frequently move to the surrounding pine timber forest.

In September, besides the areas mentioned above, large flocks may also be met with in fallows overgrown by weeds and in stubbles. These are for the most part forest enclaves or lie at the edge of cultivated fields close to a forest.

The flocks roaming about in the autumn are the largest; I often observed groups consisting of more than 50 specimens. Such abundant flocks were observed in the period when the birds did not migrate and they certainly included the specimens which had nested in the nearby region.

Not all the birds, however, gather into such large flocks. Every year single pairs are observed feeding in a chosen territory late into the autumn.

Wandering flocks behave relatively quietly, only single specimens flying over trees or uneasy about something utter alarm calls. When approaching large flocks, we may hear a note which is used by the birds as the signal to fly away. At last, one day at mid-Cotober all the flocks leave the region.

The consolidation of the young from the first brood and those of the second brood and old birds into family flocks was also observed by KOFFÁN (1960), whereas WASILEWSKI (1961) wrote about their moving to a timber forest at the time of moulting. Roving flocks watched by SCHUMANN (1959) numbered as many as 150 specimens.

XII. DEPARTURE AND WINTERING

The departure of flocks, roaming about up to this time, and single specimens occurs rather imperceptibly. The determination of the exact time of departure is difficult on account of the quiet behaviour of the birds, especially during

autumnal rains. A sudden deterioration of weather conditions accelerates the departure, night falls of temperature to below 0°C having the greatest effect in this respect, exceeding that of precipitation.

Generally speaking, Woodlarks disappear from the region under study at mid-October. In 2 cases I managed to establish the exact date of departure: October 10, 1963 and October 19, 1966. On migration the birds keep in flocks and may accompany other, more abundant aggregations of birds, such as Skylarks, Greenfinches or Chaffinches (Schumann, 1959). On fine days the birds fly high in the air, whereas they descend close to the ground under unfavourable weather conditions (Naumann, 1900). My observations suggest that the ceiling of flights does not exceed 50 m.

Not a case of wintering was observed in the Rzepin population during the 5 years of investigation, and therefore all Woodlarks fly off from this region. Their wintering in the territory of Poland was, however, recorded by Sokołowski (1936), Taczanowski (1882) and Tischler (1941). Taczanowski writes about his coming across several Woodlarks wintering in this country, one of them even sang in January. Sokołowski (1936) observed this species on January 1, when the weather was frosty and it snowed heavily. Tischler (1941) showed that Woodlarks winter in Poland more frequently than Skylarks do. Only single birds were found to winter in the countries of Eastern and Central Europe. Matoušek (1965) saw a Woodlark which wintered at a temperature of —20°C and 15-centimetre layer of snow in Czechoslovakia. Donchev (1963) reports the wintering of single specimens in Bulgaria and Volchanecky (1954) and Portenko (1954) write that the Woodlark is a stationary bird in the Crimea and Caucasus. Niethammer (1937) claims that a small number of Woodlarks winter in Germany, whereas according to Krampitz (1952), all these birds of the Frankfuhrt region fly off.

In Witherby's et al. (1948) opinion, Woodlarks do not wander in Great Britain, though in Scotland they show some local movements. Koch (1936) thinks that they are stationary and wintering birds, since their nests may be found as early as the end of March.

Like Witherby in Great Britain, in France Labitte (1958) observed only local migrations of Woodlarks and he heard singing males on winter days.

The results of ringing presented by Tischler (1941) corroborate the view that the winter quarters of Woodlarks are situated in France and South Europe.

The Woodlark is, therefore, a migrant bird in Poland and all over Central and East Europe, where only single specimens venture on wintering. On the other hand, it is a stationary bird in the west and south of Europe, where only local movements governed by the regional climatic conditions are observed. The mountainous nature of a region, e.g., in Scotland, Bulgaria, Crimea, and Caucasus, makes the birds fly away.

XIII. FOOD ACQUISITION AND MAKE-UP

The Woodlark's diet changes with the seasons, supplies of the ecological niches of the biotope which it inhabits, age of specimens, and weather conditions.

In this study I used the method of direct observation of birds, while they were foraging or feeding their young, since it interferes least with the natural course of activities observed. The advantages of this method induced me to apply it in spite of its inaccuracy. In addition, early in the spring I analysed the faeces of Woodlarks and in the nesting season I compressed the gullets of chicks according to the method described by Kluijver (1933).

Foraging birds bustle about swiftly, pecking every now and again at something among the plants and in the earth, and they are constantly on the go except for the whiles when they linger somewhat over a larger amount of food or that difficult of access. Having noticed a watcher, the male may stay motionless for 20 minutes, although its mate continues collecting food beside it. It may well be that this very ethological property is the explanation why in the population observed by Krampitz (1952) males did not feed the young at all (cf. Section X. 2, Item F).

Direct observations of birds and analyses of food brought for the young indicate that Woodlarks collect food from the surface of the ground, the uppermost layer of the soil, and the low parts of plants. Never, except for one case, when a female brooding the young tried to catch a fly flying by, did I observe a bird taking food on the fly or from a plant on which it would have had to alight. Woodlarks forage near the nest, within a radius depending on the opulence of the biotope, but not exceeding 100 m.

At first, when the feeding of nestlings is less intensive, the old birds return on foot, gathering food all the way back, up to the nest. Female No. 5 fed nearest the nest; during incubation and when fostering the young, it left the nest to a distance of hardly a few tens of centimetres and returned to it immediately after eating an insect. I watched the manner of feeding from a blind placed 0·80—2·00 m. from the nest and, therefore, I managed to recognize the parts of food hanging from a bird's bill. The results of these observations are presented in the graph in Fig. 39. Unluckily, this method involves a natural selection of observations in favour of large bits of food, too large to be held whole inside the bill. In order to obtain full data on the composition of the diet of the young, I took 72 samples of food by compressing their gullets with a ring (Kluijver, 1933) made according to the description given by Bogucki (1964). The results of determination thus obtained from 388 food fragments are presented in Fig. 40 and Table XIV.

A comparison of results obtained by both methods confirms that the observation of birds feeding their young is, as a method of food analysis, adequate in the case of beetles, butterflies, locusts, myriapods and skipjacks. There are, however, divergencies concerning the quantities of larvae of other insects,

spiders and, above all, the quantities of earthworms, which may be overestimated by many times. The error in the determination of earthworms carried out from a distance results from the technique of preparation of its prey by Woodlarks. When they catch a caterpillar, they rub it repeatedly against the earth and, consequently, all yellow-orange or brown caterpillars look from a distance like earthworms. The method based exclusively on observation, although used by many investigators, should, therefore, be treated with qualifications and completed with other, more accurate methods.

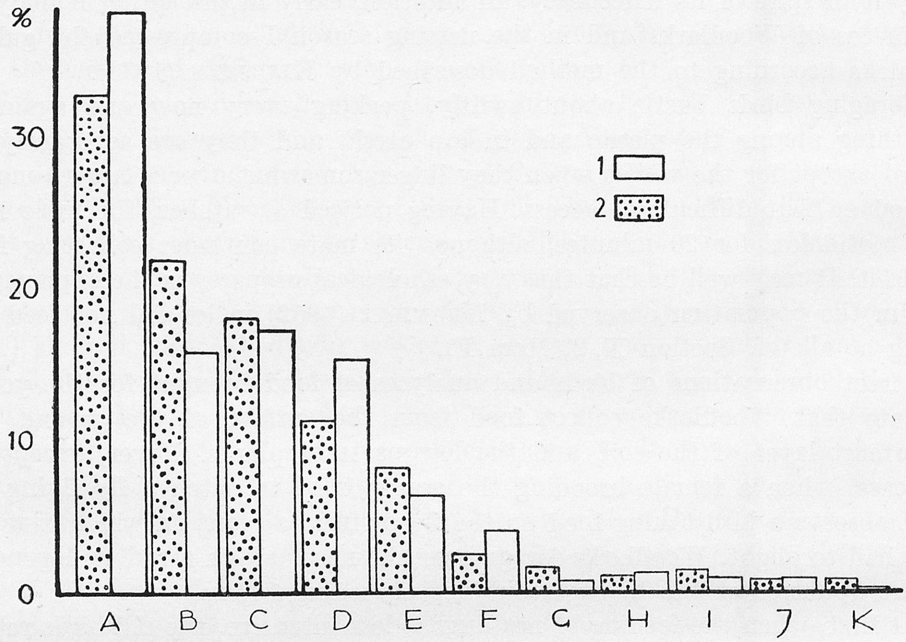


Fig. 39. Food delivered to nestlings in 8 nests by males and females, determined exclusively on the basis of observations at the time of feeding. 1 — food brought by males (N — 948 identified parts), 2 — food brought by females (N — 848 parts), A — caterpillars of butterflies, B — insect larvae undet., C — earthworms, D — beetles, E — spiders, F — butterflies (imagines), G — hymenopterans, H — grasshoppers, I — *Hylobius abietis*, J — myriapods and remaining arthropods, K — skipjacks

To estimate the mass of food rations brought to the young, the food taken from the gullets of the young of one brood and derived from 12 feedings was weighed. Its total weight was 1·91 g. Thus, the average weight of a food ration received by a nestling on the 11th day of life was 0·159 g. I also determined the size of rations using gullet rings. In 76 feedings the old birds brought, altogether, 259 food elements, i.e., various invertebrates, seeds, etc. On the average, 3·4 food elements fall to one feeding. There are, however, great deviations from the mean value, as will be seen from Table XII. Nevertheless, it appears that two-thirds of the total are portions consisting of 1—3 food elements. The mean sizes of rations on particular days of nestling life are given

in Table XIII, which shows that they generally increase with age of the birds and are smaller in the afternoon than in the morning hours.

Figure 40 shows changes in the food make-up of the young relative to the biotopes in which the nests are situated. This comparison indicates that young Woodlarks in plantations receive considerably more spiders and caterpillars but fewer germinating seeds of pine and hymenopteran larvae. Their

Table XII

Size of Food Rations Brought to the Young by Old Woodlarks

No. of Food Elements in One Feeding	1	2	3	4	5	6	7	8	9	10	...	16
No. of Feedings	13	19	17	4	9	5	1	1	2	1		1

Table XIII

The Dependence of the Size of Food Rations upon the Age of Young Woodlarks and the Time of the Day

Time of Day	Days of Life				
	7th	8th	9th	10th	11th
in the morning	3·18	—	4·16	4·80	4·00
in the afternoon	—	1·72	—	2·64	—

food lacks harvestmen. These differences result exclusively from the nature of the biotope, since in the timber forest a very abundant seeding of pine occurs every second year, and in plantations it includes only a narrow marginal tract neighbouring on the timber forest.

The presence of mosses and fallen leaves of the oak undergrowth favour the occurrence of the beetle *Byrrhus pilula*, which is considerably less numerous in plantations. A much calmer microclimate of timber forests and the presence of last year's dead leaves in the litter also create particularly favourable conditions for juvenile forms of harvestmen. Moreover, the fairly high percentage share of larvae of the pine sawfly *Diprion pini* and pine beauty *Panolis flammea* is conditioned here only by the age of the pine forest.

The appearance of pebbles in the food, parallel and proportional to the quantity of seeds consumed, is an interesting fact. As early as the beginning of the present century, Naumann (1900) emphasized that there are the more pebbles in the stomachs of old birds, the more seeds they contain. This strict interrelation is connected with the manner of digesting. It is well-known that Woodlarks do not husk seeds and therefore it becomes necessary to crush

the husks by means of pebbles. The pebbles were small fragments of limestone, 4—9 mm. in diameter.

The quantitative and qualitative differences in the food delivered on the 4th—8th days of life of the young are shown in Fig. 41. The share of seeds and pebbles increases steadily with age of the young birds. Caterpillars and similar hymenopteran larvae form a mass of constant volume, and as the number of caterpillars undergoes reduction, that of hymenopteran larvae increases.

The qualitative composition of the diet on the basis of the samples taken from the gullets of young Woodlarks and classified according to systematic

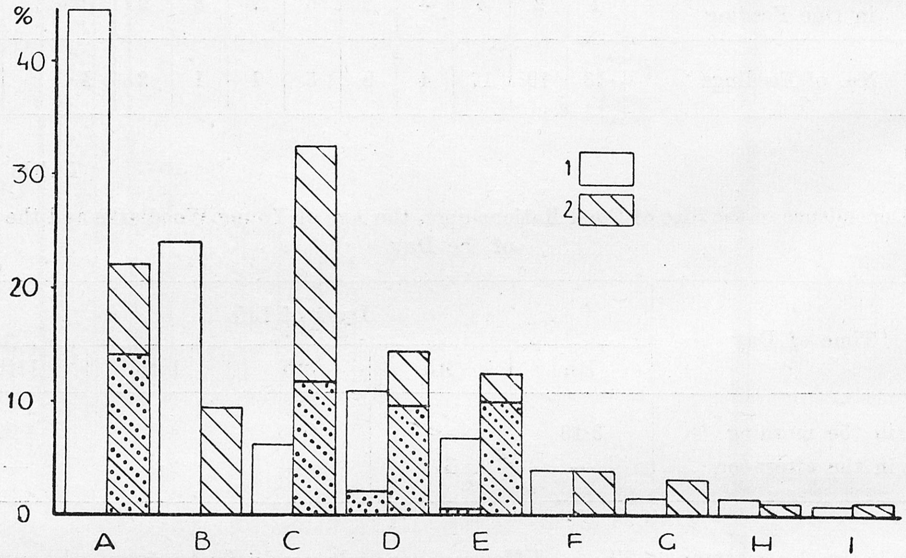


Fig. 40. The make-up of the diet of nestlings from the nests in pine plantations (1) and in gaps in pine timber forest (2), examined by the KLUIJVER method of gullet rings. A — spiders and their eggs (dotted part — *Opiliones*), B — caterpillars, C — pine seeds ans pebbles (dotted part — pebbles), D — beetles (imagines) (dotted part — *Byrrhus pilula*), E — hymenopteran, dipteran and other larvae (dotted part — *Diprion pini*), F — butterflies, hymenopterans and dipterans (imagines), G — pupae and eggs of insects, H — grasshoppers, bugs, I — myriapods and earthworms

groups is presented in Table XIV. It shows that insects formed 45·92 % of the food analysed, spiders 29·36 %, and tree seeds 16·48 %. In volume, the share of caterpillars is the largest, followed by those of spiders, beetles, other larvae, and seeds, which come in last. Other constituents of food are incidental.

Though specifically the food of the Woodlark is fairly heterogeneous, it may be stated that this bird utilizes particular constituents of the ecological niche to varying degrees. The most striking is the fact of its taking only the smallest species of weevils in plantations.

In the diet of the Woodlark beetles are represented most numerously by *Byrrhus pilula*. Like the members of the *Otiorrhynchinae*, this beetle is able to hide its appendages completely and then it resembles a spherical grain, whereas the hard and projecting appendages of weevils from the subfamily *Curculioninae* are undoubtedly awkward in the bill and less fit for the delicate gullets of young birds. Specimens of the genera *Byrrhus* and *Strophosomus* and skipjacks, taken out of birds' gullets half an hour after feeding, still had all their legs tucked under them. This property as well as the occurrence of skipjacks in the forest floor layer makes them a common element of the Woodlark's diet. The hard armour of beetles is not an obstacle since these birds are accustomed to indigestible seeds.

Myriapods, an earthworm, wireworm and larva of the ant lion met with in the food indicate that the Woodlark rummages the superficial soil layer.

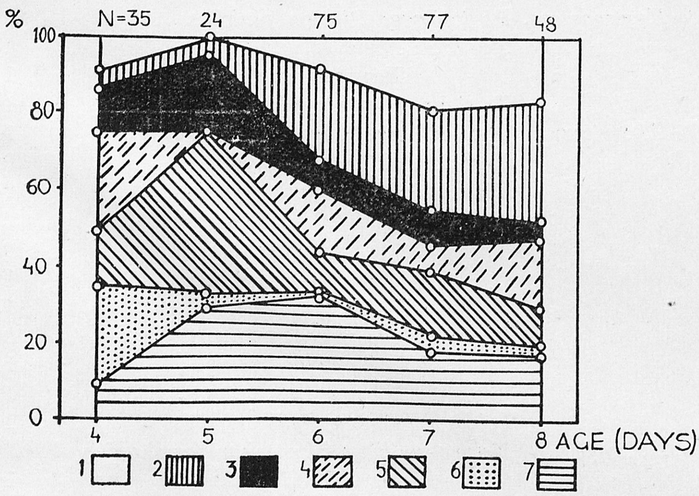


Fig. 41. Changes in the make-up of the daily food of nestlings in the period of rapid growth (4th—8th day of life) on the basis of the data from 1 nest with 6 young situated in a timber forest. The figures on the upper axis (100%) indicate the size of samples. 1 — pebbles, 2 — pine seeds, 3 — caterpillars of butterfliess, 4 — other insect larvae, 5 — beetles (imagines), 6 — imagines of other insects, 7 — spiders

This statement is also corroborated by the presence of numerous caterpillars of moths of *Agrotis* sp. which stay in soil by day, up to a depth of 3 cm.

Caterpillars of other moths (e.g., *Panolis flammea*) and larvae (e.g., *Diprion pini*) fed in the crowns of trees and were blown off them by the wind. A fairly large number (6·18%) of hairy caterpillars from the family *Noctuidae* in the food of the Woodlark is a kind of revelation, since only few species of birds feed on them. These caterpillars were in an early developmental stage and hardly up to 32 mm. in length. Their hair tufts were still well preserved. As

Table XIV

List of Food Constituents of Young Woodlarks on the Basis of the Data Obtained from the Samples Taken Using Gullet Rings

Food Constituents			No.	%
Animals:				
Annelida,	*Oligochaeta,*	*Lumbricidae*: *Lumbricus terrestris*	1	0·26
Arachnida,	*Araneida* — sp. non det.		74	19·06
	Araneida — egg deposits		4	1·03
	Opiliones — unidentified species		36	9·27
Myriapoda,	*Chilopoda* —	*Lithobius* sp.	1	0·77
	Diplopoda,	*Julidae*: *Julus* sp.	2	
Insecta,	*Saltatoria,*	*Locustidae*: unidentified larva	1	0·26
	Blattoidea,	*Phyllodromiidae*: *Phyllodromia germanica*	2	0·53
	Heteroptera, —	*Pyrrhocoris apterus*	1	0·53
		Corevideae unifentified	1	
	Hymenoptera,	*Phytophaga*: *Diprion pini* lar.	27	6·96
		Aculeata: *Formica rufa*	1	
		Formica pratensis	1	0·77
		Terebrantes: unidentified	1	
	Coleoptera,	*Melolonthinae*: *Phyllopertha horticela*	2	0·53
		Byrrhidae: *Byrrhus pilula*	29	7·46
		Elateridae: *Brachylacon murinus*	2	
		Selatosomus aeneus	2	2·58
		imago unident.	6	
		larva — wireworm	1	0·26
		Chrysomelidae: *Halticinae* unident.	1	0·26
		Curculionidae: *Strophosomus rufipes*	8	
		Phyllobius sp.	1	2·58
		species unident.	1	
		Ipidae: *Hylurgus ligniperda*	1	0·26
	Neuroptera,	*Myrmeleontidae*: *Myrmeleon formicarius* lar.	1	0·26
	Lepidoptera,	*Geometridae*: *Bupalus piniarius*	1	0·26
		unidentified lar.	1	0·26
		Noctuidae: imago, unident.	4	1·03
		larvae: *Parastichtis monoglypha*	24	
		Agrotis sp.	10	12.88
		Panolis flammea	5	
		unidentifield	11	
		pupae unidentified	3	0·77
	Diptera,	*Asilidae*: imago, unident.	3	1·03
		Tachinidae: imago, unident.	1	
		unidentified larvae	13	3·35
		unidentified pupa	1	0·26
Plants:				
Pinus silvestris — seeds, mostly germinating			64	16·42
Inorganic constituents:				
lime pebbles, 4—9 mm. in dia.			28	7·21
		Total	388	100·00

to the imagines of butterflies, Woodlarks collect only such as stay by day on the under-surface of leaves in the herb layer, chiefly members of the *Noctuidae* and *Geometridae*.

The plant food consists of pine seeds only, except for autumn and early spring, when Woodlarks consume also seeds of weeds. On their spring arrival, before any insects available to them appear, they feed exclusively on seeds of weeds, as was shown by observations and analyses of 30 samples of faeces. In addition, I often watched Woodlarks gathering seeds of *Sclerantus annuus*.

The analysis carried out above indicates the influence exercised by the presence of Woodlarks in a stand on its state of health. The greater part of its food consists of harmful or indifferent arthropods. Although the Woodlark rummages the floor layer, it does not consume useful insects of the families *Cincidelidae* and *Carabidae*, probably because of their long and hard legs. The removal of caterpillars of *Panolis flammea* and larvae of *Diprion pini*, fallen to the forest floor, is, no doubt, to the great advantage of the forest. The limitation of occurrence of *Strophosomus rufipes* and members of the genus *Agrotis* is also of some importance, which is best illustrated by the fact that the inspection of 60 trap groves made for catching caterpillars of this last insect near the nests in plantations gave only negative results in the course of 2 years.

The data from literature show that the share of insects and other arthropods in the Woodlark's diet is generally larger than in the case of other larks (NAUMANN, 1900; SOKOŁOWSKI, 1936; NIETHAMMER, 1937). NAUMANN (1900) mentions beetles and their larvae, small locusts and flies as its prey. Stomach analyses of 3 birds killed in May (BAER, 1909 — after NIETHAMMER, 1937) revealed the presence of numerous beetles of the family *Curculionidae*, one grasshopper and a large quantity of seeds of pine and knotgrass. STEINFATT (1939), who observed the feeding of the young, lists the following animals which go to the making of their food, in the order of quantity: caterpillars (probably including larvae of sawflies), beetles, flies (among others, tabanids), small butterflies, spiders (twice), a small dragonfly and 2 small snails. In Poland the problem of diet was dealt with only by SOKOŁOWSKI (1936), who found insects, spiders and a small quantity of seeds in the Woodlark's food.

The observations of STEINFATT (1939) and HARRISON and FORSTER (1959) concerning the radius within which this bird collects food agree with those presented in this paper.

On the basis of the present results it may be stated that a pair of Woodlarks bring the young of an average brood an average of 3660 invertebrates weighing about 170 g. This quantity of food is collected and supplied to the young in the course of 11 days and it does not include the food of the old birds themselves. Seeing that species harmful from the viewpoint of silviculture form a great proportion of the Woodlark's food, the role played by this bird is not indifferent.

XIV. REGULATION OF POPULATION

Ornithologists differ in their views on the number of broods reared by Woodlarks. NIETHAMMER (1937), STEINFATT (1939) and TISCHLER (1941) claim that these birds have 2 broods regularly and do not rule out the possibility of a third brood. They try to support their opinion by such facts as the long song period of males and the presence of nests as late as July. On the other hand, SCHUSTER (1939) quotes the statistical data given by HAUN (1931) for 99 nests, of which only 15 fell in June and one in July. SCHUSTER (o. c.) quotes also the data from the catalogue of the nido-oological collection of the Koenig Museum, showing that out of the 44 clutches in the possession of the collection only 5 were taken in June and again one in July. KRAMPITZ (1952) writes about the occurrence of one brood only.

I obtained similar results in my study. All the nests observed by me represented spring breeding. Only two cases are suspected to represent second broods. Rare instances of repeated breeding generally begin towards the end of May and at the beginning of June, as shown by the following examples. Female No. 6 left its nest on April 27, 3—4 days before the term of hatching. I saw this female sitting on a repeated clutch as late as June 6. Another female, No. 24, left 2 addled eggs on April 30 and the young of its repeated brood hatched as early as May 31. Thus, the young which hatch in the first half of June are, as a rule, from repeated broods. Disturbances in taking possession of the territory as well as in the selection of nest site cause that part of the females may retard egg laying by nearly 3 weeks. These facts explain the rearing of broods in June and July, there being no need to adopt the rule that Woodlarks breed twice a year; on the contrary, it may be assumed that in the Rzepin population this happens rarely. The biology of all Woodlarks in Central Europe, undoubtedly, presents itself in a similar manner (KRAMPITZ, 1952).

In southern Europe the Woodlark may have more broods. Twofold breeding (from April till mid-May and in June) is reported by MATOUŠEK (1965) from Czechoslovakia, DONCHEV (1963) from Bulgaria, and PORTENKO (1954) from the U.S.S.R. Owing to the marking of birds, KOFFÁN (1960) managed to confirm the occurrence of second broods in Hungary. He also often observed repeated broods after the destruction of the first nest and only in one case out of the 160 pairs and 280 nests examined the successful rearing of 3 broods. He established the average interval between the laying of the first egg of the first brood and that of the first egg of the second brood to be 42·2 days.

On the basis of the now presented materials the mean clutch size is 3·97 eggs, from which 3·08 young birds hatch, and only 1·85 leave the nest. Assuming that 10% of these birds rear a second brood, the annual increase is 2·04 young per pair. Observations of other relative species, however, show that a half of these young birds perish (BERNDT, MEISE, 1965). The total increase in the population would therefore be about 0·5 young per 1 sexually

Table XV

Causes of Losses in the Broods of Woodlarks in Various Periods of Nesting

Causes of destruction or loss	Developmental periods: egg laying	incubation		hatching		nestling stage		departure from nest		Total of losses according to their causes	
	No. of nests	No. of eggs (N = 107)	%	No. of young (N = 83)	%	No. of young (N = 65)	%	No. of young (N = 55)	%	No. of eggs and/or young (N = 107)	%
Rain				4	4·8			3	5·5	7	6·5
Sun's rays				5	6·0					5	4·7
Low temperature				1	1·2					1	0·9
(Total of abiotic causes)				(10)	(12·0)					(13)	(12·1)
Red-backed Shrike						5	7·7			5	4·7
Jay						4	6·2			4	3·7
Trampled by female				1	1·2					1	0·9
(Total of bird causes)				(1)	(1·2)	(9)	(13·9)			(10)	(9·3)
Man	2	15	14·0			1	1·5			16	14·9
Unidentified factors		10	9·3					2	3·6	12	11·2
Addled eggs				7	8·4					7	6·5
Total of losses	2	25	23·3	18	21·6	10	15·4	5	9·1	58	54·0

Percentages in particular developmental periods are calculated in relation to the total number of specimens at the begining of given developmental period.

mature bird yearly. Assuming the mean longevity of Woodlarks to be 4 years, the decrease in this period would be 2 birds. Such a low degree of reproduction of the Woodlark may partly explain its irregular occurrence and low density in the biotopes which are suitable for this species.

Only a few out of the great number of factors that reduce the population size during the nesting season were observed in the course of this study. Their share in this respect is presented in Table XV. These factors are as follows: weather conditions — 12·1 %, birds — 9·3 %, man — 14·9 %. The cause of destruction was not determined in 11·2 % of the total of eggs laid, and the addle eggs formed 6·5 %.

In the first group the most damage was caused by rains (6·5 %) and the least by low temperatures (0·9 %). These factors had a particularly bad effect at the time of hatching of the young, especially if the female was disturbed and could not warm them appropriately. Long lasting rains at the time when the young leave the nest are also very dangerous.

Birds were the most harmful of the animals, especially the Red-backed Shrike *Lanius collurio* — 7·7 % and the Jay *Garrulus glandarius* — 6·2 %. They plundered nests in which there were fairly large young birds, killing 13·9 % of them. However, the Red-backed Shrike did not always notice a nest, even if this was situated no more than 12 m. from the tree in which it regularly perched.

The highest percentage of the damage was caused by man (nearly 15 % of the eggs laid). Damage is, however, unavoidable, though observation be carried out in as circumspect a manner as possible. Woodlarks are most sensitive to the presence of an observer at the beginning of the nesting season. Under natural conditions, with no interference of observers, this percentage is undoubtedly lower.

The losses diminish gradually as the process of nesting advances. The proportion of eggs destroyed in the incubation period was 23·4 %, whereas the destruction at the time of hatching formed 21·6 %. The number of the young killed in the nestling stage constituted 15·4 % and that at the time of their leaving the nest 9·1 % of all the young observed in the given period.

More than 25 % of the nests examined contained 1 addled egg each, irrespective of the clutch size, since in the largest clutch of 6 eggs no egg was addled and 1 addle egg was found in a three-egg clutch.

Nest parasites, especially *Dermanyssus avium*, too, may reduce the resistance of the young and thus increase their mortality rate. Other harmful animals are included in the group of unidentified factors (11·2 %) and they are chiefly mammals. In the biotopes under study Woodlarks are threatened for the most part by foxes, stray cats, hedgehogs, and small rodents.

XV. SOME MODES OF BEHAVIOUR

The preceding sections dealt, above all, with the ecology and reproduction of the Woodlark. It remains to discuss various modes of its behaviour, such as modes of walking, drinking water and bathing, sleeping out of the nest, and behaviour in unfavourable weather conditions and in the presence of mammals as well as other species of birds.

1. Modes of Walking

When feeling safe, the Woodlark runs cringing very fast and stops only to get food or make sure of its safety. Disturbed by an approaching observer or changes in the surroundings, it moves rhythmically, stopping every now and again, and its mode of moving resembles that of a displaying pigeon. Then it shuffles with its neck craned and drops a curtsy every several steps, retracting its neck rapidly and slightly raising the tail to keep its balance. This manner of walking combines the desire to reach the destination quickly and to observe the surroundings with the readiness to run away.

2. Drinking of Water and Bathing

Being originally steppe birds, the Alaudidae are not closely associated with water. The amount of water which they acquire in their food or in the form of dew and rain-drops, drunk off the grass blades, is sufficient. I observed a female Woodlark drinking water drops off the plants surrounding the nest each time it rained or after the rain. Woodlarks occasionally drink water also from puddles.

At the time of autumnal migrations Woodlarks and Skylarks may be allured by means of a special mirror, described and figured by Naumann (1900). Revolving round its axis, such a mirror sends reflexes into the space and these appear to the birds as reflections of the sunlight from water or dew-drops (Pätzold, 1963). As steppe birds, larks do not bath in water, but they very often take sandbaths. The purpose of such baths is to get rid of parasites, but Krampitz (1952) observed that they may often be an expression of excitement of a displaying male. Bathing places are distributed all over the region, where the sand is loose and has no admixtures of humus.

3. Roosting out of the Nest

In the section concerned with the choice and occupation of territory I have already mentioned about the distribution of roosts and the situation of future nests in relation to them.

Roosts are recognized by clots of faeces, about 20 in number in particular cases, accumulated in one place. A close analysis of such places showed that Woodlarks sleep squeezed in between twigs of very small pines or grass blades, which cover them from behind. They always have their heads directed towards the west (WSW). Analogical data on the roosting of the Crested Lark *Gallerida cristata* are presented by Abs (1963). In the case of both these birds the orientation of the body is conditioned by the light of the setting sun. During one season a bird roosts in turn in several places, which is probably connected with weather conditions.

4. Behaviour under Unfavourable Weather Conditions

Precipitation is the most influential of the meteorological phenomena in the breeding season. During heavy rains the birds gave up feeding, became inactive, puffed out their plumage and shrank their necks. On the other hand, drizzle did not prevent them from foraging. Incubating females outwore a spell of snow on the nest and let themselves be covered with snow completely except for their heads. The hail, as big as a pea, made a male take shelter in a young stand of pines, whereas its mate continued incubating and stood to its post throughout the hail storm. Lightning and thunder had no visible effect on the behaviour of birds, which, in one case, did not react even to a stroke of lightning at a distance of 100 m. from the nest. Their sensibility to the big noise made by jetplanes passing the sound-barrier, gunshots at a distance of 300 m., and whistle of a railway engine was also very small. The incubating female always became uneasy at the first noise, but got used to them in an extremely short time. Fog and hoar frost have a evident effect on the time of awakening, delaying it by more than an hour in the morning.

5. Behaviour towards Mammals

Single observations were made as to the behaviour of Woodlarks towards mammals. A hare foraged in the vicinity of nest No. 15 every day, coming sometimes to a distance of 3 m. from the nest, without any responses on the part of the birds. However, when it approached the nest at the time of their absence, the returning pair of birds showed great anxiety. When a roe appeared 10 m. from the nest, its presence did not rouse fear of the birds. The male, perching in a low watch-tree, did not stop singing, though the roe approached somewhat nearer.

6. Behaviour towards Birds

The presence and voices of birds which may be dangerous to Woodlarks paralyse their movements. The appearance of the Goshawk, Buzzard, Marsh Harrier, Cuckoo, Jay, and Red-backed Shrike make them stay motionless

and crouched close to the ground. At the sight of a Cuckoo a female kept this position for 23 minutes and when it was on the nest, it was much on the alert for these dangerous species. A repeated appearance of a bird of prey made Woodlarks partly familiar with its presence, e.g., pair No. 18 reared their brood successfully under a Red-backed Shrike's eyes.

The following species of birds frequented the areas occupied by Woodlarks: Great Spotted Woodpecker, Black Woodpecker, Blackbird, Linnet, Tree Pipit, Skylark, Wheatear, Starling, Mistle Thrush, Song Thrush, Swallow, Redstart, Hoopoe, and others. A sudden appearance or low flight of any of these birds near the nest rendered the female uneasy. Their alarm calls always released impulses of fear and alertness in Woodlarks. Males often replied to them also by uttering alarm calls and females looked about intently.

Woodlarks responded most to the alarm calls of such birds as the Great Spotted Woodpecker, Blackbird, Mistle Thrush, and Swallow, flying over their territory. These voices always woke the female from its nap and caused its long inspection of the region.

In three cases I observed conflicts with birds of other species. Twice they were fights with a Starling and once the chasing of a Yellow Hammer away from the neighbourhood of the nest. The fight with a Starling was started when at the time of arrival of the Woodlarks with food it came up to a distance of 50 cm. from the nest. The male attacked the Starling, flying just over it. The fight consisted in uttering notes of anger by both birds, flying no more than 50 cm. over each other, and assuming fierce attitudes. Finally, the tired birds stopped fighting. However, when the Starling noticed a caterpillar hanging from the Woodlark's bill, it attacked this last in order to snatch away its prey, but the attitude of threat assumed by both Woodlarks, the male and female, made the Starling fly off.

Translated into English
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STRESZCZENIE

Przedmiotem niniejszej pracy jest biologia skowronka borowego, populacji zamieszkującej bory sosnowe Puszczy Rzepińskiej. W latach 1962—1966 objęto badaniami 51 par tych ptaków i 31 gniazd. Przy 11 gniazdach prowadzone były obserwacje ciągłe, od świtu do zmierzchu, w bezpośrednim sąsiedztwie gniazda (fot. 1) przez 575 godzin w czasie wysiadywania jaj i 1240 godzin w okresie karmienia piskląt.

Obserwowana populacja w większości gnieździła się na zalesionych porębach leśnych. Rosły tam prócz posadzonych sosenek różne rośliny, stanowiące m. in. osłonę gniazd skowronków borowych (tabele I i II).

Powrót z zimowisk następuje zwykle w pierwszej połowie marca (od 21. II. do 17. III.), zawsze w kilka dni po przylocie skowronka polnego, po całkowitym stopieniu się pokrywy śnieżnej na bezdrzewnych powierzchniach (tabela III). Stada ciągowe szybko rozwiązują się i samce zajmują terytoria. Nawroty

zimy powodują ponowne łączenie się stad i zbliżanie się z terenów leśnych do wsi. Powierzchnie terytoriów gniazdowych, które samce bronią przed rywalami, mają 2—3 ha. Są one trzykrotnie większe od terytoriów skowronków polnych. O wyborze terytorium gniazdowego lub pokarmowego decydują: 1) wysokość drzewek porastających powierzchnię zalesioną — u sosny optymalne warunku istnieją na zalesieniach 2-letnich, podczas gdy uprawy 7-letnie są już omijane (ryc. 1), 2) obecność drzew obserwacyjnych — najczęściej są to drzewa z otaczającego wylesioną powierzchnię lasu, 3) wielkość otwartej powierzchni — wśród zwartych starych lasów musi ona wynosić przynajmniej 2 ha.

Samce sygnalizują zajęcie terytorium śpiewem. Wyróżnia się u nich 5 rodzajów śpiewu: śpiew w locie, nadrzewny, naziemny, w czasie gonitwy i śpiew zaniepokojenia. 3 pierwsze, analizowane były dokładniej. Na podstawie powtarzających się motywów można wyodrębnić 5 różnych zwrotek. Najczęściej skowronek borowy śpiewa zwrotki z motywem „*dlidlidli...*", a najrzadziej trel (ryc. 2). Ilość motywów w jednej zwrotce waha się od 5 do 12 (tab. IV), a długość trwania zwrotki 4—19 sekund (tab. V). W następstwie zwrotek brak prawidłowości (tab. VI). Samce, które nie posiadają jeszcze samic śpiewają najintensywniej (do 94 min. jeden śpiew — por. ryc. 5), głównie w locie (ryc. 3) i najwyżej — do 100 m nad ziemią. Z chwilą połączenia się w pary intensywność i długość śpiewu samca maleje (ryc. 4 i 5). Obniża się również wysokość lotu podczas śpiewu do 50 m. Śpiew na drzewie jest najbardziej typowy dla samców, których samice wysiadują jaja (ryc. 3). Na ziemi samce śpiewają najrzadziej — tylko przed okresem inkubacji. W ciągu doby najintensywniej skowronki borowe śpiewają rano. Śpiew w czasie gonitwy usłyszeć można jedynie podczas przepędzania innych osobników z bronionego terytorium. Śpiewem zaniepokojenia reagują samce m. in. na zbliżanie się obserwatora do pary, która znajduje się w pobliżu gniazda. Samice również śpiewają, krótkie zwrotki, gdy zmuszone przez samca chwilowo opuszczają gniazdo. Wpływ popędów na formy śpiewu przedstawia tabela VII. Popęd płciowy najsilniej ujawniają samce śpiewem w locie i śpiewem gonitwy. Terytorializm wiąże się ze śpiewem nadrzewnym i również śpiewem gonitwy. Samce przestają śpiewać, gdy rozpoczynają karmienie piskląt. Jesienią, po połączeniu się w stada i przy sprzyjających warunkach atmosferycznych, samce znowu śpiewają jak na wiosnę, tylko krócej (do 28 min.) i częściej na drzewie.

W zależności od brzmienia i okoliczności, w jakich samiec i samica wydają głosy, można ich wyodrębnić 6: wabiący, ostrzegawczy, niepewności, lęku, gniewu i stadny.

W zachowaniu się seksualnym samca wobec samicy można wyróżnić: rytmiczne podrywanie skrzydeł, ukłony, odwracanie się od samicy, obroty, rozpościeranie ogona z opuszczaniem skrzydeł i kopulację. Wobec rywali samiec stroszy pióra stojąc na wyniosłościach gruntu, przepędza intruza i toczy walki. Samice poza postawą gotowości do kopulacji nie wykazują innych zauważalnych przejawów zachowania się seksualnego.

Wybór miejsca na gniazdo poznać można po częstym przebywaniu obu ptaków w tej części terytorium i nocowaniu w pobliżu. W większości przypadków terytoria gniazdowe i pokarmowe się pokrywają. W mniej dogodnych warunkach sąsiadują z sobą.

Na położenie gniazda największy wpływ ma wysokość drzewostanu otaczającego bezdrzewną zajmowaną przestrzeń. 80% badanych gniazd znajdowało się w odległości do 4 wysokości drzewostanu, a maksimum przypadało na odległość 2 wysokości drzew od skraju drzewostanu (ryc. 8). Z tych odległości kąt widzenia drzewostanu, tj. kąt między linią horyzontalną, a linią łączącą oko wysiadującego ptaka z wierzchołkami drzew waha się w granicach 15—45° (ryc. 7).

Skowronek borowy umieszcza gniazdo pod kępą turzycy, trawy lub pod drzewkiem (tab. 2). Wyboru miejsca dokonuje samica. Budowę gniazda rozpoczynają ptaki wydrążeniem dołka w ziemi. Na przekroju ma on kształt paraboloidy o bardziej prostopadłych ściankach przy twardym podłożu (ryc. 9). Średnica dołka waha się w granicach 95—120 mm × 73—127 mm, a głębokość 34—73 mm. Samiec i samica drążą równocześnie, każde swój oddzielny dołek. Jedna para wykonuje 2—4 dołków, z których jeden jest wybrany do budowy gniazda. Gniazdo buduje wyłącznie samica — rola samca sprowadza się do czuwania nad bezpieczeństwem. Dla każdego nowego lub powtórzonego lęgu samica buduje nowe gniazdo, najczęściej w którymś z wykopanych uprzednio dołków. Samica zbiera materiał w pobliżu gniazda, a następnie lecąc lub idąc znosi go do gniazda. W miarę postępu budowy spada częstotliwość znoszenia materiału, a wzrasta intensywność formowania wnętrza gniazda (ryc. 10 i 11, tabela VIII). Odbywa się ono przez wejście samicy do wnętrza gniazda i przyciskanie piersi do brzegu, przy jednoczesnym dreptaniu nóżkami po przeciwnej stronie. Obraca się ona przy tym wokół osi gniazda. Samica zaczyna budowę od brzegów gniazda, a dno buduje na końcu (ryc. 13).

W strukturze gniazda wyróżnić można trzy warstwy: podkładową (z grubszych, zdrewniałych części roślin i z mchu), konstrukcyjną (głównie z traw) i wyścielającą (wyłącznie z drobnych korzonków) (ryc. 14). Włosy zostały znalezione tylko w 2 gniazdach. Ptaki dochodzą do gniazda z jednej strony. Według stron świata dojście usytuowane jest od NW—NE (ryc. 12).

Pierwsze jajo zostaje zniesione jeszcze w trakcie budowy lub po pewnej przerwie (do 3 dni). Każde następne jajo znosi samica w 24-godzinnych odstępach. Znoszenie jaj odbywa się w godzinach rannych (6—9^{45}). Wielkość pełnego zniesienia waha się od 2 do 6 jaj (tab. IX). Wielkość i kształt jaj odpowiada opisom ze Środkowej Europy. Waga jaj świeżego wynosi 2.99—4.00 g i spada sukcesywnie w miarę upływu czasu wysiadywania. Na ogół cięższe jaja więcej tracą na wadze niż lżejsze (ryc. 15). Wysiadywaniem zajmuje się wyłącznie samica. Rola samca ogranicza się do czuwania nad bezpieczeństwem samicy w pobliżu gniazda i w czasie żerowania. W 80% przypadków samica przerywa wysiadywanie na wyraźne wabienie samca. Później powraca z nim razem lecąc i lądując w odległości do 6 m od gniazda. Po każdym wejściu na

gniazdo dokonuje półobrotu i siada dziobem skierowana do wejścia. Wysiadująca samica zapada w krótkie drzemki, wypatruje niebezpieczeństw, poprawia układ jaj, wygładza wnętrze gniazda przez obroty i usuwa pasożyty. Częstotliwość tych czynności w ciągu całego okresu inkubacji ilustruje ryc. 16. Samica skowronka borowego wysiaduje wyjątkowo „twardo" (Fot. 8). Wrażliwość na przeszkody spada w miarę zbliżania się momentu wykłucia się piskląt (ryc. 17). Spłoszona z gniazda samica stara się zwieść wroga, lecąc niewysoko nad ziemią, trzepocząc skrzydłami i rozpościerając w sposób charakterystyczny ogon.

Wysiadywanie rozpoczyna się w lęgach 5-jajowych już po zniesieniu 4-go jaja — w lęgach mniejszych po zniesieniu ostatniego jaja. Noc samica w tym okresie spędza zawsze na gnieździe. W ciągu dnia przerywa natomiast wysiadywanie w celu zdobycia pożywienia. Przerwy w wysiadywaniu są początkowo dłuższe i skracają się w miarę zbliżania się wykłucia piskląt (ryc. 19). Ilość przerw w ciągu dnia natomiast utrzymuje się mniej więcej na tym samym poziomie przez cały okres wysiadywania. Średni czas każdego wysiadywania maleje od chwili przebudzenia się o świcie aż do godz. 10—11, a po osiągnięciu tego minimum wzrasta aż do zaśnięcia wieczorem. Wielkość przerw w wysiadywaniu nie zależy od pory dnia (ryc. 21). Podobnie więc przedstawia się intensywność godzinowa wysiadywania (ryc. 20).

Okres wysiadywania kończy się w 13—15 dniu. Świeżo wykłute pisklę zauważa samica najczęściej (w 80% przypadków) dopiero w chwili powrotu do gniazda z żerowania. Skorupki jajowe usuwają skowronki borowe zwykle przez połykanie ich zaraz przy gnieździe. Rozpiętość czasu między wykłuciem się pierwszego i ostatniego pisklęcia dochodzi do 18 godzin.

W ciągu niespełna 1 godziny po wylęgu samica rozpoczyna karmić pisklęta. Samiec aczkolwiek karmi je też od pierwszego dnia, rozpoczyna zawsze później od samicy. W ogromnej większości przypadków całą porcję pokarmu otrzymuje każdorazowo jedno pisklę. Ilość karmień wzrasta z każdym dniem. Do ósmego dnia życia jedno pisklę otrzymuje przeciętnie 200 porcji pokarmu (ryc. 22). Maksymalna ilość karmień wszystkich piskląt w ciągu 1 dnia wynosiła 244 razy. Globalną ilość karmień w ciągu przebywania piskląt w gnieździe kształtują: ilość piskląt, ilość dni ich przebywania w gnieździe oraz indywidualna intensywność karmienia danej pary. Częstotliwość karmień zmienia się z wiekiem piskląt (ryc. 24). Wpływ wielkości lęgu na częstotliwość karmień ilustruje ryc. 22. W lęgach czerwcowych częstotliwość karmień spada w stosunku do lęgów majowych. Wydłużanie się dnia powoduje rozpoczynanie karmień coraz wcześniej przed wschodem słońca i kończenie ich coraz później po zachodzie. W ciągu doby wahania częstotliwości karmień są znaczne (ryc. 25), wykazują jednak 2 charakterystyczne maksima: poranne i wieczorne. W miarę wzrostu piskląt ptaki dorosłe coraz więcej czasu poświęcają w ciągu dnia zbieraniu pokarmu. Czas potrzebny dla zebrania pełnej porcji pokarmowej na uprawach sosnowych wynosi ok. 8 min.

Udział samców w karmieniu piskląt jest zależny od rozwoju piskląt i pory

dnia. Aczkolwiek samica rozpoczyna karmienie, samiec już w pierwszym dniu karmi częściej i jego przewaga utrzymuje się do 4-go dnia — później samiec i samica karmią prawie równie często (ryc. 27). Zbiorczo jednak udział samca w karmieniu jest minimalnie mniejszy od udziału samicy. W ciągu doby najintensywniej samce karmią rano, gdy samice pożywiają się same po nocnym ogrzewaniu piskląt (ryc. 28).

Wydalane odchody usuwają karmiące ptaki podobnie jak skorupki jaj przez połykanie albo przez wynoszenie poza gniazdo. Do 6 dnia życia piskląt przeważa połykanie odchodów, w następnych zaś wynoszenie. Im więcej jest piskląt w gnieździe, tym szybciej ustępuje forma usuwania odchodów przez połykanie na korzyść wynoszenia (ryc. 30). Samiec wynosi do 5. dnia życia piskląt więcej odchodów, a później mniej od samicy (ryc. 31). Ilość wydalanych odchodów wzrasta do 6. dnia życia i utrzymuje się na tym poziomie do 11. dnia, by potem stopniowo się zmniejszać (ryc. 29). Przeciętnie 3 karmienia przypadają na jedno wydalanie odchodów. Skowronki borowe wynoszą prócz skorup jaj i odchodów również i martwe pisklęta, jaja zepsute pozostawiają natomiast w gnieździe.

We dnie samice poza karmieniem chronią pisklęta przed zimnem, deszczem i zbytnią insolacją (fot. 16). Długość czasu ogrzewania zależy od wieku piskląt i ich ilości (ryc. 33 i 34). Ogrzewanie w ciągu dnia ustaje prawie zupełnie w lęgach o 5 i 4 pisklętach w 5. dniu, o 3 pisklętach w 6. dniu, a w lęgach z dwoma pisklętami w 8. dniu. W nocy samica ogrzewa je natomiast zwykle do 8. dnia. Każdorazowy silniejszy opad atmosferyczny samice spędzały zawsze na gniazdach, chroniąc pisklęta w ten sposób przed zmoczeniem. Po opuszczeniu gniazda pisklęta jednak nie chronią się pod samicę i w deszczowej pogodzie często giną. Opieka samicy nad pisklętami polega również na usuwaniu pasożytów. Ponadto kilkakrotnie stwierdziłem walkę samicy z gąsiorkiem w obronie piskląt i specyficzną postawę wobec kukułki.

W rozwoju piskląt można wyróżnić 3 okresy: wzrostu postembrionalnego, wzrostu szybkiego i powolnego. Najintensywniejszy wzrost wagi przypada na 2. okres tj. 3—11 dzień życia piskląt (ryc. 35). O wzroście wagi piskląt decyduje ilość karmień i wielkość kęsów. W dużych lęgach stosunki pod tym względem są niekorzystne (tab. XI). Zwiększony metabolizm spowodowany stratami cieplnymi zmniejsza również przyrost wagi piskląt w lęgach o 2 pisklętach, mimo większej ilości karmień. Dobowy przyrost ciężaru piskląt w dniach 4—7 utrzymuje się na tym samym poziomie (ryc. 36), co powoduje systematyczny spadek względnego przyrostu ciężaru (ryc. 38). W tym samym gnieździe zróżnicowanie ciężaru poszczególnych piskląt jest nieznaczne, gdyż pisklęta najlżejsze po 2 dniach osiągały największe przyrosty i tym samym wyrównywały swój niedobór wagi (ryc. 37). Świeżo wykłute pisklę waży 2.00—3.07 g i jest pokryte 133 piórami puchowymi w 13 oddzielonych od siebie polach. Zajady są siarkowo-żółte. W gardzieli widać 4 ciemne plamki (fot. 9). Ciało początkowo woskowo-żółte przebarwia się w ciągu 5 dni z wierzchu na szarawy kolor, a od spodu na cielisto-różowy. Od 5. dnia życia pisklęta

widzą. W 8. dniu pierwsze pióra przebijają stosiny. Bezpierzki brzucha przykryte są przez pióra dopiero w 11. dniu życia (fot. 17). W 13. dniu pisklę ma całkowicie wykształcone upierzenie młodociane, różniące się od szaty ptaków dorosłych żółtawą obwódką pokryw grzbietowych i okrągławym plamkowaniem na piersi. Pisklęta początkowo zwrócone są głowami do środka gniazda; od 5. dnia głowy mają zwrócone w kierunku z którego nadchodzą stare ptaki z pokarmem. Od 9. dnia wychodzą już z gniazda naprzeciw karmiącym rodzicom. Najwcześniej wychodzą naprzeciw pisklęta w lęgach niedokarmionych (np. przy 5—6 pisklętach). Opuszczają gniazdo między 10 a 13 dniem życia. Płoszone opuszczają gniazdo wcześniej (nawet 8 dnia). Zwykle wszystkie pisklęta opuszczają gniazdo prawie równocześnie.

W pierwszych dniach po wyjściu z gniazda wszystkie ptaki przebywają na tym samym terenie. Z chwilą uzyskania przez młode zdolności do lotu, przemieszczają się początkowo na żerowiska leśne, a jesienią przebywają w biotopach obfitujących w chwasty. Stadka rodzinne łączą się przed odlotem w coraz większe grupy. Odlot w okolicach Rzepina następuje zwykle w drugiej dekadzie października.

Pokarmem skowronków borowych są głównie owady i nasiona chwastów i drzew iglastych. Zbierają go z powierzchni ziemi i nisko położonych części roślin. Wydziobują również pokarm przykryty cienką warstwą ziemi. Dla piskląt zbierają go w promieniu do 100 m od gniazda. Z odległości 0.8—2.0 m obserwator może rozpoznać większość zwisających z dzioba kęsów. Zestawienie wyników tych obserwacji przedstawia ryc. 39. Wyniki analizy pokarmu piskląt zdobytego metodą Kluijvera (1933) przez uciskanie przełyków, przedstawia tabela XIV i ryc. 40 i 41. Ilościowo największą grupę stanowią pajęczaki. Wśród owadów przeważają stadia larwalne (szczególnie motyli) — w stadium imago najwięcej było różnych chrząszczy. Skład pokarmu zależy m. in. od wieku otaczającego tereny lęgowe drzewostanu. Przeciętny ciężar porcji pokarmu wynosił 0.159 g. Wielkość porcji wzrasta z wiekiem piskląt i przed południem jest większa niż po południu (tab. XIII). Z wiekiem piskląt następują zmiany w składzie ich pokarmu. Przybywa, kosztem pokarmu zwierzęcego, ilość pokarmu roślinnego i wraz z nim ilość kamyków ułatwiających rozcieranie nasion (ryc. 41).

Większość par wyprowadza tylko 1 lęg — częste jest jednak powtórzenie pierwszego lęgu po stracie. Średnia wielkość lęgu wynosi 3.97 jaj. Z tego wykłuwa się 1.08 piskląt, a tylko 1.85 opuszcza gniazdo. Ogólnie (razem z rzadko występującymi drugimi lęgami) średni przyrost roczny wynosi 2.04 piskląt na parę ptaków przystępujących do rozmnażania. Wśród czynników redukujących populację wymienić można niekorzystne warunki atmosferyczne, drapieżnictwo ptaków i niszczącą działalność człowieka.

W opisach różnego sposobu zachowania się zwrócono uwagę na charakterystyczne sposoby chodzenia zaniepokojonego ptaka, picie wody, kąpiele piaskowe oraz noclegowiska. Noclegowiska rozpoznać można po skupieniu dużej ilości odchodów w jednym miejscu. Skowronki borowe poza gniazdem śpią

skulone pod osłoną roślin, zwrócone głową w kierunku zachodzącego słońca. Opady atmosferyczne przetrzymują skurczone przywierając do ziemi i tylko w jednym obserwowanym przypadku większy grad zmusił samca do schowania się pod okapem młodych sosenek. Samice na gnieździe wytrzymywały wszelkie burze, grady, a nawet przysypanie 3-centymetrową warstwą śniegu. Obecność w pobliżu ptaków i ssaków nie zagrażających życiu skowronków borowych (np. sarna, zając) nie niepokoi ich. Reagują natomiast znieruchomieniem na obecność jastrzębia, myszołowa, błotnika stawowego, kukułki, sójki i dzierzby gąsiorka. Głosy ostrzegawcze innych ptaków wywołują u skowronków borowych odruchy zaniepokojenia i czujności.

РЕЗЮМЕ

Предметом настоящей работы является биология юлы (лесного жаворонка), популяции обитающей в сосновом бору Жепинской пущи. В 1962—1966 гг. исследовано 51 пару этих птиц и 31 гнездо. При 11 гнездах проводились постоянные наблюдения от рассвета до сумерок, в непосредственном соседстве гнезда (фот. 1) через 575 часов во время высиживания на яйцах и 1240 часов во время кормления птенцов.

Наблюдаемая популяция в большинстве случаев гнездилась на облесенных лесных засеках. Кроме посаженных сосен там росли различные растения, защищая гнёзда юлы (табл. I и II).

Возвращение из зимовок обычно происходит в 1 половине марта (от 21. II до 17. III), всегда несколько дней позже прилёта полевого жаворонка, после полного таяния снежного покрова на безлесных площадях (табл. III). Перелётные стада быстро распадаются и самцы занимают территории. Возвращение зимы вызывает повторное объединение стад и приближение их из лесных территорий к деревне. Площади гнездовых территорий, которые самцы обороняют перед соперниками составляют 2—3 га, т. е. втрое больше чем полевых жаворонков. О выборе гнездовой территории решают: 1. высота деревьев, растущих на облесенной площади — у сосны оптимальные условия существуют на облесенных двугодичных площадях, тогда как 7-летние культуры они обходят (фиг. 1), 2. присутствие наблюдательных деревьев — чаще всего это деревья из леса, окружающего безлесную лесную поверхность, 3. величина открытой поверхности — среди густых старых лесов она должна составлять не менее 2 га.

О оккупировании территории самцы сигнализируют пением. У них отмечено 5 видов пения: пение на лету, на дереве, на земле, во время бега и во время беспокойства. Три первых пения проанализировано более обстоятельно. На основании повторяющихся мотивов можно выделить 5 различных куплетов. Чаще юла поёт куплеты с мотивом „длидлидли“..., а реже всего „трръь“... (фиг. 2). Количество мотивов в одном куплете колеблется от 5 до 12 (табл. IV), а продолжитель-

ность одного куплета 4—19 секунд (табл. V). В последовательности куплетов нет закономерности (табл. VI). Самцы, у которых нет ещё самок поют наиболее интенсивно (до 94 мин. одно пени—ср. фиг. 5), главным образом на лету (фиг. 3) и наиболее высоко — до 100 м над землёй. С момента соединения пары интенсивность и длина пения самца уменьшается (фиг. 4 и 5). Понижается также высота полёта во время пения до 50 м. Наиболее типичным является пение на дереве для самцов, которых самки высиживают на яйцах (фиг. 3). На земле самцы поют реже всего — только перед инкубацией. В течении суток наиболее интенсивно юла поёт утром. Пение во время пробега можно услышать лишь при прогонах иных особей из защищаемой территории. Пением беспокойства реагируют самцы, между прочим, на приближение наблюдателя к паре, находящейся вблизи гнезда. Самки также поют короткие куплеты, когда самцы заставляют их на кратковременный отход от гнезда. Влияние полового влечения на формы пения представлено в таблице VII. Самцы проявляют половое влечение наиболее сильно пением на лету и пением гонки. Территориальность связана с пением на дереве и с пением гонки. Самцы прекращают петь, когда начинают кормить птенцов. Осенью, после соединения в стада, при благоприятных атмосферных условиях самцы опять поют, как весной только короче (до 28 минут), и чаще на дереве. Можно выделить 6 голосов в зависимости от обстоятельств и звучания, в которых самец и самка издают их: привлекательный, предостерегающий, неуверенный, пугливый, гнева и стайный.

В половом поведении самца в отношении к самке можно выделить: ритмическое вздёргивание крыльями, поклоны, отворачивание от самки, обороты, простирание хвоста с опусканием крыльев и копуляцию. К соперникам самец взъерошивает перья, стоя на возвышенности земли, прогоняет пришельца и ведёт бои. У самок кроме позиции готовности к копуляции, других половых проявлений не обнаружено.

Выбор места на гнездо можно узнать по частым пребываниям пары на данной части территории и ночевании их вблизи. В большинстве случаев гнездовые и кормовые территории совпадают. В менее благоприятных условиях они находятся по соседству.

На расположение гнезда наибольшее влияние имеет высота древостоя, окружающего занимаемую территорию, лишённую деревьев. 80% исследованных гнёзд находилось на расстоянии до 4 высот древостоя, а максимум приходилось на расстоянии 2 высот деревьев от опушки леса (фиг. 8). Из этих расстояний угол видимости, т. е. угол между горизонтальной линией и линией соединяющей глаз, высиживающей птицы, с верхушками деревьев колеблется в пределах 15—45° (фиг. 7).

Юла вьёт гнездо под пучком осоки, травы или под деревцом (табл. 2). Выбор места делает самка. Строение гнезда начинают птицы из выдалбливания лунки в земле. Его сечение имеет форму параболоиды при более перпендикулярных стенках на твёрдом субстрате (фиг. 9). Диаметр лунки колеблется в пределах 95—120 мм × 73—127 мм, а глубина 34—73 мм. Самец и самка „выкапывают" по одной лунке. Одна пара делает 2—4 лунки, из которых одну выбирают на по-

строение гнезда. Гнездо строит только самка. Самец же караулит её. Для каждого нового или повторяемого высиживания самка строит новое гнездо, чаще всего в одной из сделанных лунок. Самка собирает материал вблизи гнезда, а затем летит или идёт и несёт его к гнезду. Со временем частота сноса материала падает и возрастает интенсивность формирования внутренней части гнезда (фиг. 10 и 11, табл. VIII). Это происходит путём входа самки во внутрь гнезда и прижимания груди к краю, при одновременном топтании ножками по противоположной стороне. При этом она поворачивается вокруг оси гнезда. Самка начинает строение от краёв гнезда, а наконец его дно (фиг. 13).

В строении гнезда можно выделить 3 слоя: основной (из более толстых, одеревеневших частей растений и из мха), конструкционный, главным образом из трав, и выстилающий (исключительно из мелких корешков) (фиг. 14). Волосы найдено лишь в 2 гнёздах. Птицы доходят к гнезду с одной стороны. Подход осуществляется из северо — запада к северо — востоку (фиг. 12).

Первое яйцо самка сносит во время строения гнезда или после небольшого перерыва (до 3 дней). Каждое следующее яйцо самка сносит из суточными промежутками. Кладка яиц происходит в утренние часы ($6—9^{45}$). Величина полной кладки колеблется от 2 до 6 яиц (табл. 9). Величина и форма яиц соответствует описанию из Средней Европы. Вес свежего яйца составляет 2.99—4.00 г и последовательно падает со временем высиживания. В общем, более тяжёлые яйца теряют больше на весе чем лёгкие (фиг. 15). Высиживает исключительно самка. Роль самца ограничивается к присматриванию за безопасностью самки вблизи гнезда и во время добывания пищи. В 80% случаев самка прерывает высиживание на отчётливую приманку самца. Затем возвращается вместе с ним и приземляется на расстоянии до 6 м от гнезда. После каждого входа в гнездо проделывает пол-оборота и садится клювом по направлении к входу. Самка во время высиживания коротко дремлет, высматривает опасность, поправляет расположение яиц, выглаживает внутреннюю часть гнезда оборотами и удаляет паразитов. Частоту этих действий на протяжении всей инкубации показано на фиг. 16. Самка юлы высиживает исключительно „твёрдо". Чувствительность на преграды падает по мере сближения момента вылупления птенцов (фиг. 17). Вспуганные самки при гнезде пытаются обмануть врага, летая невысоко над землёй, трепетая крыльями и раскладывая свойственным образом хвост.

Высиживание начинается после кладок, состоящих из 5 яиц уже после 4 яйца, а в кладках меньших после конечного яйца. В этот период самка ночь проводит всегда в гнезде. Днём же она, на некоторое время, покидает гнездо в поисках корма. Перерывы в высиживании вначале длиннее, сокращаются по мере сближения момента вылупления птенцов (фиг. 19). Количество перерывов днём удерживается почти на одинаковом уровне через весь период высиживания. Средняя продолжительность времени каждого высиживания уменьшается от момента пробуждения на рассвете до 10—11 часов, а после достижения этого минимума возрастает до погружения в сон вечером. Количество перерывов в высиживании не зависит от времени дня (фиг. 18). Похожей кажется часовая интенсивность высиживания (фиг. 20).

Период высиживания заканчивается к 13—15 дню. Свежевылупившихся птенцов самка замечает чаще всего (в 80% случаев) лишь в момент возврата к гнезду из добычи корма. Яйцевые скорлупы юла удаляет обычно путём глотания их при гнезде. Промежуток времени между вылуплением первого и последнего птенца доходит до 18 часов.

Почти через час после вылупления птенца самка начинает его кормить. Хотя самец кормит их также с первого дня, но он начинает всегда позже самки. В подавляющем большинстве случаев целую порцию корма получает каждый раз один птенец. Количество кормлений возрастает с каждым днём. К 8 дню жизни один птенец получает в среднем 200 порций корма (фиг. 22). Максимальное количество кормлений всех птенцов на протяжении 1 дня составляло 244 раза. Общее количество кормлений в течении пребывания птенцов в гнезде определяют: количество птенцов, время пребывания их в гнезде и индивидуальная интенсивность кормления данной пары. Частота кормления изменяется с возрастом птенцов (фиг. 23). Влияние величины выводка на частоту кормлений иллюстрирует фигура 24. В июньских выводках частота кормлений падает в сравнении с майскими. Удлинение дня вызывает учащение кормлений перед восходом солнца и заканчивание их всё позже после запада. Колебания частоты кормлений на протяжении суток являются значительными (фиг. 25), однако обнаруживают 2 характерные максимума: утренние и вечерние. По мере роста птенцов взрослые птицы всё больше времени на протяжении дня посвящают добычи пищи. Время, необходимое на сбор полной кормовой порции, на сосновых плантациях составляет около 8 минут.

Участие самцов в кормлении птенцов зависит от развития птенцов и времени дня. Хотя самка начинает кормление, самец уже в первый день кормит чаще и его перевес удерживается до 4 дня. Затем самец и самка кормят почти одинаково (фиг. 27). В сумме, самец кормит, однако, незначительно меньше самки. На протяжении сутки самцы кормят утром, когда самки ищут корм после ночного согревания птенцов (фиг. 28).

Экскременты удаляют кормящие птицы так же, как яичные скорлупы, путём глотания или выноса из гнезда. До 6 дня жизни птенцов преобладает глотание экскрементов, а затем их вынос. Чем больше птенцов в гнезде, тем быстрее уступает форма удаления экскрементов глотанием на пользу выноса (фиг. 30). Самец выносит больше экскрементов до 5 дня жизни птенцов, а затем меньше чем самка (фиг. 31). Количество выделяемых экскрементов возрастает до 6 дня жизни и удерживается на этом уровне до 11 дня, а затем постепенно уменьшается (фиг. 29). В среднем 3 кормления приходятся на одно выделение экскрементов. Юла удаляет, кроме яичных скорлуп и экскрементов, также мёртвых птенцов, но испорченные яйца оставляет в гнезде.

Днём самки, кроме кормления, охраняют птенцов от холода, дождя и лишней инсоляции (фот. 16). Продолжение времени согрева зависит от возраста птенцов и их количества (фиг. 33 и 34). Согревание на протяжении дня почти совсем прекращается в выводках с 5 или 4 птенцами на 5 день, а с 3 птенцами на 6 день, в выводках с 2 птенцами на 8 день. Ночью же самка согревает их обычно до 8 дня.

Во время сильных атмосферных осадков самки сидели всегда на гнёздах, охраняя птенцов перед промоканием. Птенцы, покинув гнездо, однако, не прячутся под самкой и во время дождевой погоды часто гибнут. Несколько раз я наблюдал за боем самки юлы с сорокопутом в обороне птенцов и характерную позу в отношении к кукушке.

В развитии птенцов можно выделить 3 периода: постэмбрионального роста, быстрого и медленного роста. Наиболее интенсивный рост приходится на второй период т. е. на 3—11 день жизни птенцов (фиг. 35). О росте веса птенцов решает количество кормлений и величина комка пищи. Большие выводки по этому поводу являются невыгодными (табл. XI). Увеличенный метаболизм, вызванный потерей тепла, уменьшает также прирост веса птенцов в выводках с 2 птенцами, несмотря на большее количество кормлений. Суточный прирост веса птенцов на 4—7 день удерживается на одинаковом уровне (фиг. 36), что вызывает систематическое снижение относительного прироста веса (фиг. 38). В одном гнезде дифференциация веса отдельных птенцов незначительна ибо самые лёгкие птенцы после 2 суток достигали наибольших приростов и тем самым выравнивали недостаток веса (фиг. 37). Птенец, сразу же после вылупления, весит 2.00—3.07 г и покрыт 133 пуховыми перьями в 13, отделённых от себя, полях. Заеды серожёлтые. В глотке видны 4 тёмные пятнышка (фот. 9). Тело вначале восково-жёлтое и в течении 5 дней сверху изменяется на сероватый цвет, а снизу на телесно-розовый. На 5 день жизни птенцы видят. На 8 день первые перья пробивают стержни. Части брюшка покрываются перьями лишь на 11 день жизни (фот. 17). На 13 день птенец имеет полностью сформированное оперение, отличающееся от оперения взрослых птиц жёлтой каёмкой спинного покрова и почти круглыми пятнышками на груди. Птенцы вначале обращены головами к средине гнезда, а с 5 дня в направлении прилёта кормящих птиц. На 9 день выходят с гнезда на встречу кормящим родителям. Слишком рано так встречают родителей не докормленные птенцы (при 5—6 птенцах). Они покидают гнездо между 10 и 13 днём жизни. Испуганные покидают гнездо быстрее (даже на 8 день). Обычно все птенцы покидают гнездо одновременно.

В первые дни после выхода из гнезда все птицы находятся в одной местности. С момента приобретения возможности летать, птенцы летят за кормом в лес, а осенью находятся в биотопах богатых в сорняки. Родительские стайки объединяются перед отлётом всё в большие группы. Отлёт в окрестностях Жепина происходит обычно во второй половине октября.

Юла питается преимущественно насекомыми, семенами сорняков и хвойных деревьев. Корм собирают из поверхности земли и низко расположенных частей растений. Могут выклёвывать также корм прикрытый тонким слоем земли. Для птенцов собирают его в радиусе до 100 м от гнезда. Из расстояния 0,8—2,0 м наблюдатель может видеть довольно хорошо большинство свисающих из клюва кусков корма. Сопоставление итогов этих наблюдений представляет фигура 39. Итоги анализа корма птенцов добытых по методу Клюйвера (1933) путём нажима на пищевод, показывает таблица XIV и фигуры 40, 41. По количеству, наибольшую группу составляют паукообразные. Среди насекомых преобладают личиноч-

ные стадии (особенно бабочек) — в стадии имаго преобладали различные жуки. Состав пищи зависит, между прочим, от возраста древостоя, окружающего выводковые местности. Средний вес кормовой порции составлял 0,159 г. Величина порции увеличивается с возрастом птенцов и перед полуднем она больше, чем после полудня (табл. XIII). По мере роста птенцов изменяется также состав их корма. Со временем, количество животного корма уменьшается, а растительного увеличивается вместе с камушками, облегчающими растирание семян (фиг. 41).

Большинство пар лишь один раз выводят птенцов. Однако после гибели выводка самка часто повторяет кладку. Средняя величина кладки составляет 3,97 яиц. Из них вылупляется 1,08 птенцов и только 1,85 покидает гнездо. В общем (вместе с редко встречающимися повторными кладками) средний годичный прирост составляет 2,04 птенцов на пару птиц, приступающих к размножению. Среди факторов редуцирующих популяцию, следует назвать неблагоприятные атмосферные условия, хищничество птиц и человека.

В описаниях поведения птиц обращено внимание на характерные способы хождения, питье воды, купание в песке и ночевание. Ночёвки можно узнать по большом количестве экскрементов в одном месте. Юла вне гнезда спит скорченная под растительным прикрытием, обращена головой в направлении заходящего солнца. Атмосферные осадки выдерживают скорченные к земле. Только в одном, наблюдаемом случаев, большой град заставил самца к прятке под навесом молодых сосенок. Всякие бури, грады и даже присыпку 3-см слоем снега выдерживали самки в гнезде. Присутствие вблизи птиц и млекопитающих, не угрожающих жизни юлы (нпр. косуля, заяц) не беспокоит их. При появлении ястреба, канюка, камышевого луня, кукушки, сорокопута жулана они замирают. Остерегающие голосы других птиц вызывают у юлы рефлекс беспокойства и бдительности.

PLATES

Plate XII

Phot. 1. A blind situated in the close neighbourhood of a nest, which is marked with a stick set in the ground

Phot. 2. A pre-breeding roost, marked by the presence of compact clods of feaces



Phot. 1

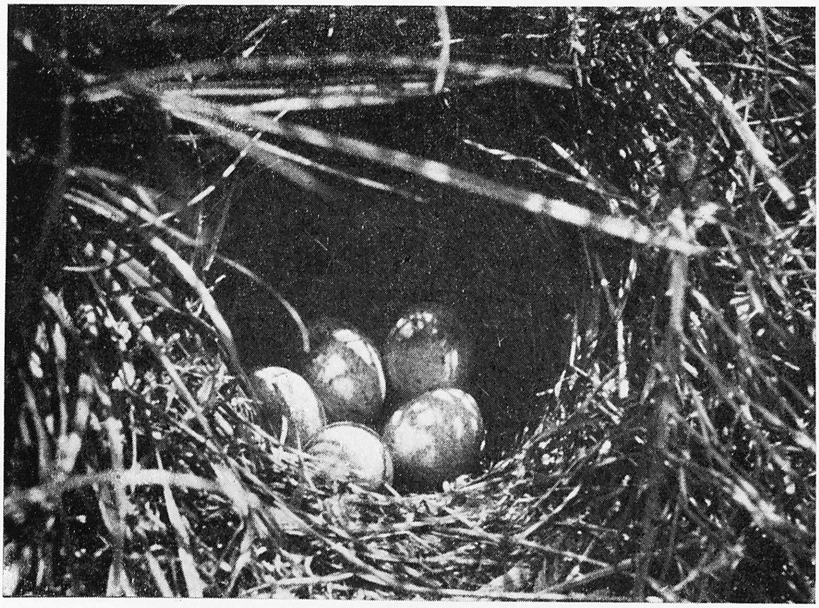


Phot. 2

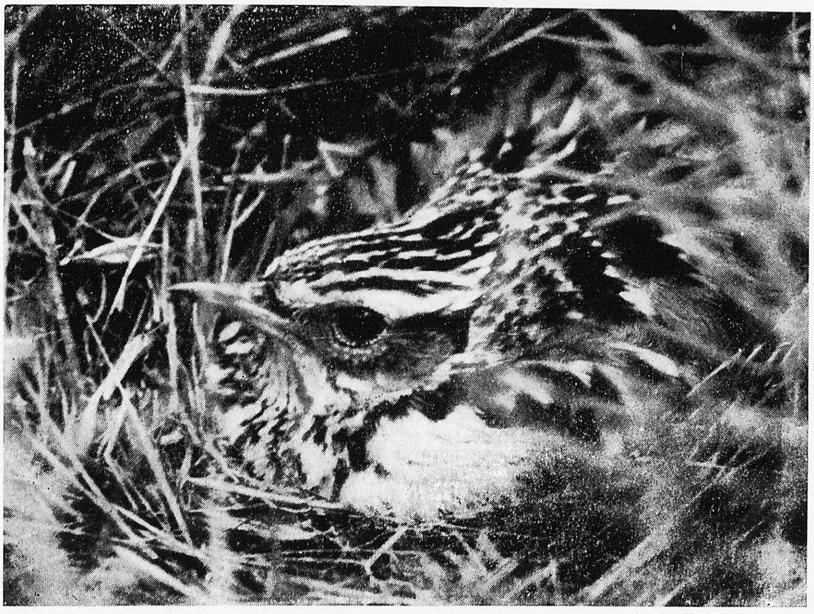
R. Mackowicz
Phot. author

Plate XIII

Phot. 3. A Woodlark's nest with a full clutch of 5 eggs
Phot. 4. An incubating female Woodlark



Phot. 3



Phot. 4

R. Mackowicz
Phot. author

Plate XIV

Phot. 5. An incubating female in the posture of anxiety

Phot. 6. An incubating female on the watch for an enemy from the air (a Jay that was flying over)



Phot. V



Phot. VI

R. Mackowicz
Phot. author

Plate XV

Phot. 7. A female romoving parasites from its feathers on the nest

Phot. 8. A touch of the bill of the female in the last phase of incubation does not release the impulse to fly away



Phot. 7



Phot. 8

R. Mackowicz
Phot. author

Plate XVI

Phot. 9. The hatching of young Woodlarks
Phot. 10. A male Woodlark carrying an egg-shell away from the nest after the hatching of a young



Phot. 9



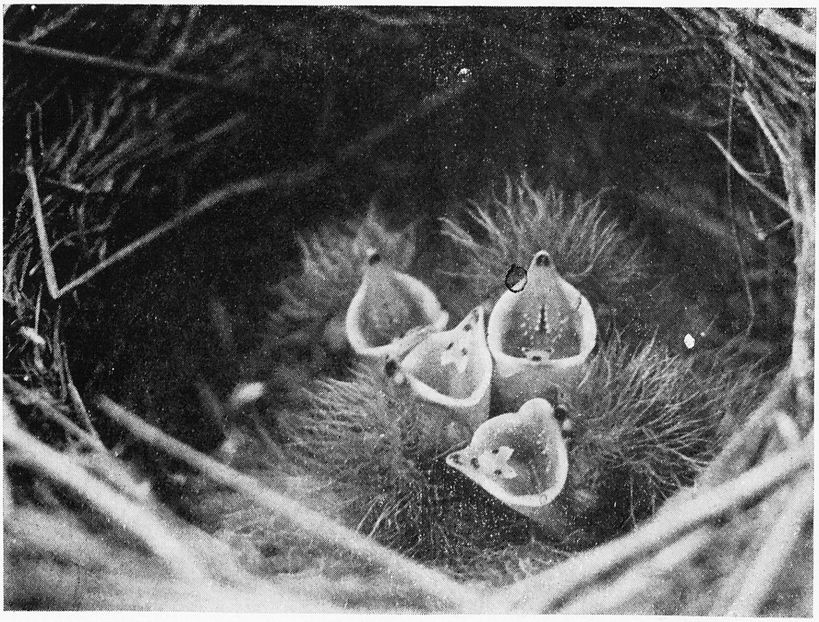
Phot. 10

R. Mackowicz
Phot. author

Plate XVII

Phot. 11. Four-day-old Woodlark nestlings in the nest

Phot. 12. Common feeding of the young in the nest by the female and male (there are 4 nestlings in the nest)



Phot. 11



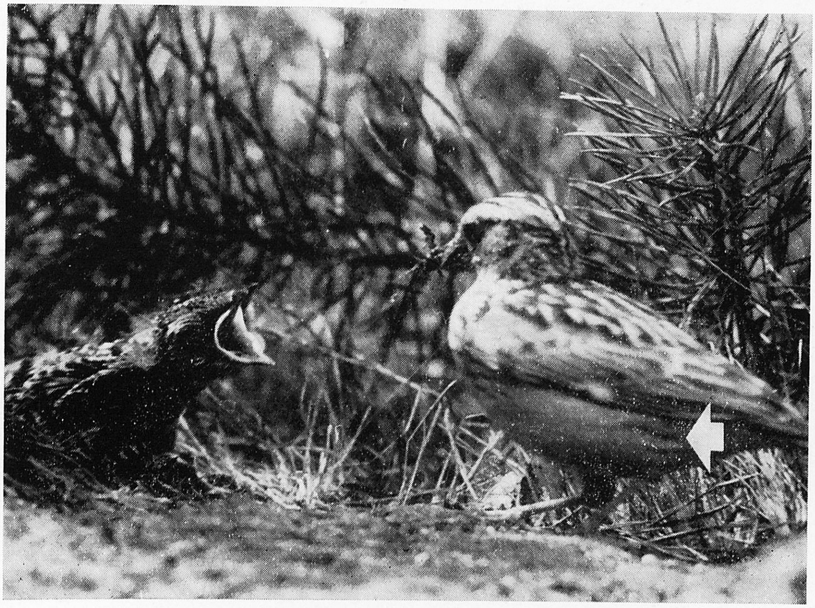
Phot. 12

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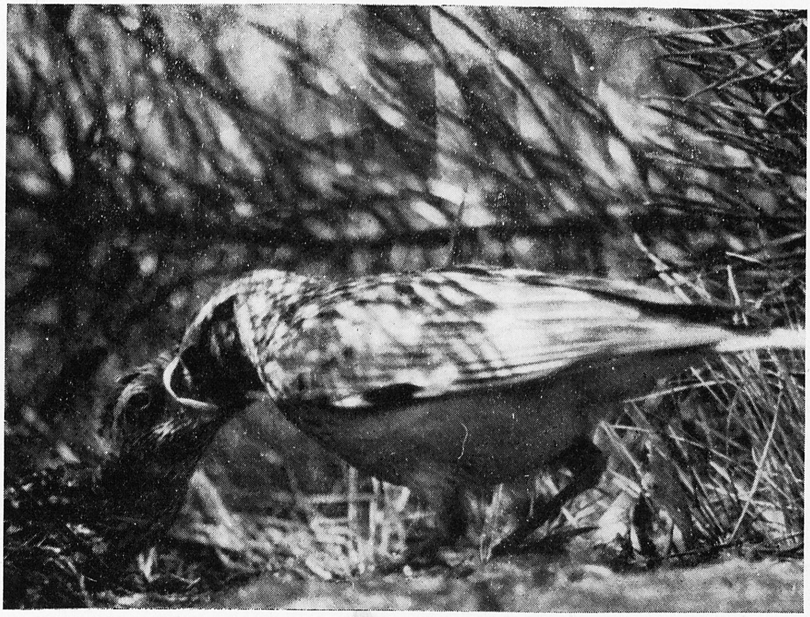
Plate XVIII

Phot. 13. A female Woodlark approaching the nest with an 8-day-old nestling coming off the nest to meet it. The arrow indicates a distinctive character of the female Woodlark: 2—4 dark feathers on the flank of the posterior part of the belly

Phot. 14. A male Woodlark feeding a nestling (lack of dark feathers which are characteristic of the female)



Phot. 13

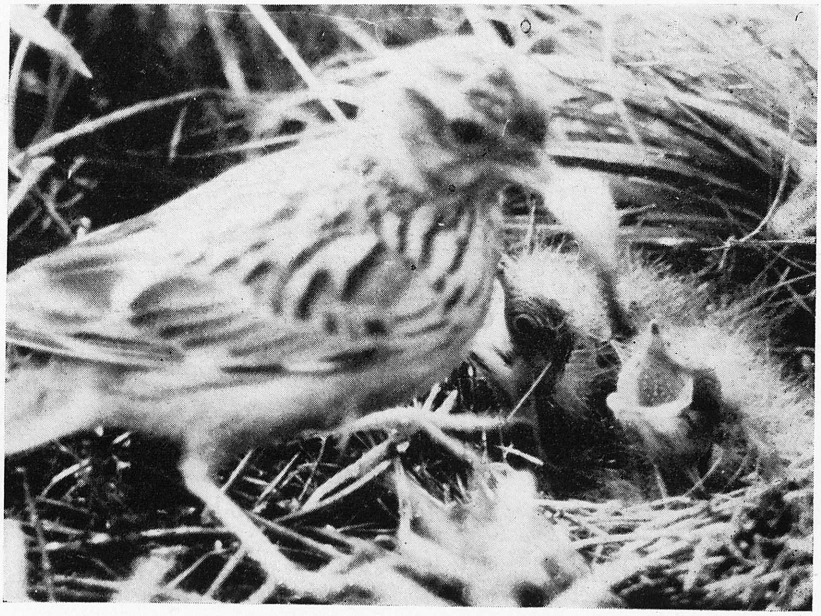


Phot. 14

R. Mąckowicz
Phot. author

Plate XIX

Phot. 15. A female Woodlark removing feaces of the young from the nest
Phot. 16. A female Woodlark sheltering the young against the strong solar radiation



Phot. 15

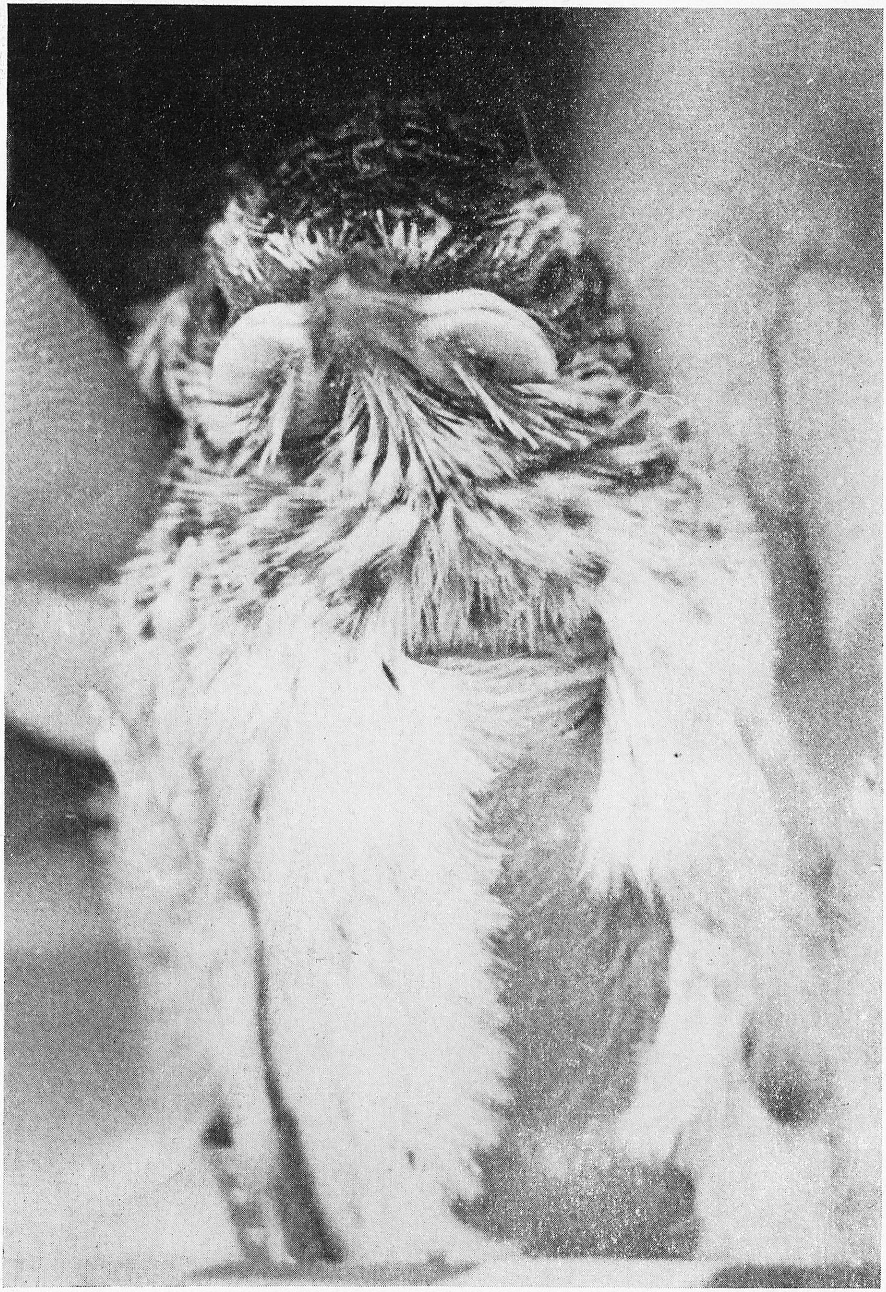


Phot. 16

R. Mackowicz
Phot. author

Plate XX

Phot 17. Nine-day-old Woodlark nestling. The abdominal apteria are conspicuous



Phot. 17

R. Mackowicz
Phot. author

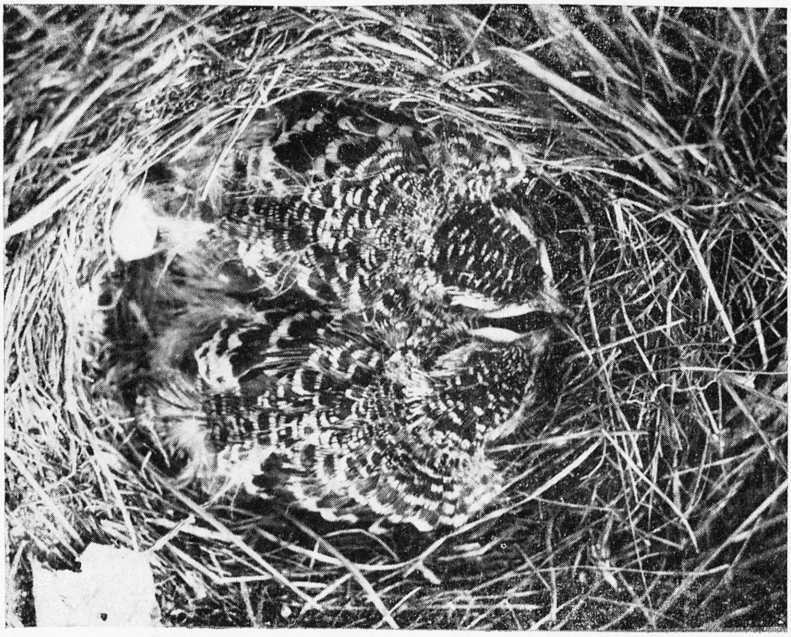
Plate XXI

Phot. 18. A female clearing parasites avay, immediately after feeding the young

Phot. 19. Two Woodlark nestlings fill up the whole nest-cup on the last day of their stay in the nest



Phot. 18



Phot. 19

R. Mackowicz
Phot. author

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